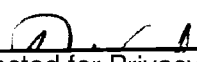



AN ABSTRACT OF THE THESIS OF

Steven D. Gehman for the degree of Master of Science in  
Wildlife Science presented on December 8, 1983.

TITLE: Activity Patterns and Behavior of Free-living Nuttall's  
Cottontails   
Redacted for Privacy

Abstract Approved:  B. J. Verts

Population attributes, behavior, and activity patterns of Nuttall's cottontails (Sylvilagus nuttallii) inhabiting a juniper-sagebrush scabland community in central Oregon were studied between June 1980 and August 1981. Cottontails were trapped, marked for individual recognition, and released at their sites of capture. Data collected by periodic trapping and censusing of cottontails on the study area indicated that population densities, and rates of natality and survival of cottontails were similar to those that occurred during the preceeding 8 years on the same area.

Behavioral and environmental data were collected during systematic observation periods conducted on a selected portion of the study area, and during cruises that covered the entire 116-ha study area. Postures, body movements, and behaviors exhibited by Nuttall's cottontails were cataloged and compared with those reported for other leporids. Observed behaviors were classified into the following categories: feed, rest, locomote, groom, tree-climbing activities, interspecific interactions, transitional acts, coprophagy, vocalizations, reproductive social interactions, and nonreproductive

social interactions. Of 1,192 behavioral acts recorded during 352 h of systematic observation, 92.9% represented nonsocial behaviors and accounted for 92.6% of the total time cottontails were in view. Behavior of cottontails appeared to be directed towards maintenance of favorable energy balance; when in view during daytime hours, cottontails spent most of their time feeding (58.5%) and resting (23.0%). Nuttall's cottontails were observed to climb in juniper trees, and this behavior was believed to be an adaptation for acquiring water in times of moisture stress. Adult social behavior was observed only during the reproductive season, and accounted for a relatively small portion (7.4%) of the activity budget of cottontails.

Indices of cottontail activity were examined in relation to reproductive condition of cottontails collected near the study area and to environmental conditions at the time of observation. Correlation coefficients and principal component analysis suggested the absence of a single dominating environmental influence on cottontail activity patterns. Seasonal variation in activity of adult cottontails, particularly males, was related to reproductive condition; activity increased from the second through fourth breeding periods then declined during the last breeding period within the reproductive season. A dramatic decline in activity of adult males corresponded with regression of testes among cottontails collected nearby and with cessation of breeding.

Nuttall's cottontails exhibited a bimodal pattern of daily activity that appeared related to temperature and moisture

requirements of rabbits and combinations of environmental constraints that influenced those requirements. An early morning peak of activity corresponded with increasing ambient temperatures and near-maximum plant water content; activity reached a low point during midday, when air temperatures often were above the zone of thermoneutrality for rabbits and water availability was minimal; an evening peak of activity that corresponded to more favorable air temperatures may be related largely to metabolic demands for energy.

Activity Patterns and Behavior of Free-living  
Nuttall's Cottontails

by

Steven D. Gehman

A THESIS

submitted to

Oregon State University

in partial fulfillment of  
the requirements for the  
degree of

Master of Science

Completed December 8, 1983

Commencement June 1984

APPROVED:

Redacted for Privacy

~~Professor of Wildlife Ecology in charge of major~~

Redacted for Privacy

~~Head of Department of Fisheries and Wildlife~~

Redacted for Privacy

~~Dean of Graduate School~~

Date thesis presented

December 8, 1983

Typed by LaVon Mauer for

Steven D. Gehman

## ACKNOWLEDGEMENTS

I thank B. J. Verts, B. E. Coblentz, A. R. Blaustein, and D. deCalesta for their professional advice, guidance, and critical reviews of this thesis. I am grateful to D. Niess, D. McIntire, R. G. Anthony, and N. T. Weiss for statistical consulting provided during the course of this research. I also thank the following friends and students who assisted in various aspects of this project: K. Hundertmark, G. Hundertmark, C. Scafidi, N. T. Weiss, G. Green, A. Cargill, W. Smith, K. Meier, B. Hollaman, T. Lum, L. Ling, D. Dahlstrom, B. Benson, D. O'Loughlin, K. Jensen, H. Coe, J. Barchie, and D. Higgins.

This research was funded in part by the Oregon Agricultural Experiment Station, Project 902. The Committee on Computing Time for Un-sponsored Research at Oregon State University provided a grant for computer services.

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# ACTIVITY PATTERNS AND BEHAVIOR OF FREE-LIVING NUTTALL'S COTTONTAILS

## INTRODUCTION

Nuttall's cottontails (Sylvilagus nuttallii) inhabit the intermountain region of the western United States and southwestern Canada (Hall, 1981); however, knowledge of their behavior, ecology, and life history is incomplete. Understanding of the biology of the species has come largely from descriptive accounts (Bailey, 1936; Orr, 1940; Janson, 1946; Hall, 1951; Ingles, 1965), and from recent studies of reproduction, population dynamics, habitat utilization, genetics, and food selection and juvenile survival of Nuttall's cottontails in central Oregon (Powers and Verts, 1971; McKay and Verts, 1978a, 1978b; Skalski and Verts, 1981; Hundertmark, 1982).

Published knowledge of behavior within the family Leporidae consists mainly of scattered field observations (Vorhies and Taylor, 1933; Brown, 1935; Beule, 1940; Hamilton, 1940; Orr, 1940; Southern, 1940, 1948; Ingles, 1941; Beule and Studholme, 1942; Ecke, 1955; Rowley and Mollison, 1955; Lowe, 1958; Hunt, 1959), and observations of animals confined in small pens (Grange, 1932; Dalke, 1942; Severaid, 1942; Hendrickson, 1943; Lord, 1964; Brenner and Flemming, 1979). The only detailed published account of leporid behavior based on observations of free-ranging individuals was provided by Lechleitner (1958), who described and classified behavioral patterns of black-tailed jackrabbits (Lepus californicus).

Observations of European wild rabbits (Oryctolagus cuniculus) in Australia by Mykytowycz (1958) and Myers and Poole (1959) represent the first attempts to study behavior of rabbits intensively in

relatively large field enclosures. By use of similar enclosures, Marsden and Conaway (1963) conducted a preliminary study of adult social interactions in eastern cottontails (Sylvilagus floridanus), and Marsden and Holler (1964) followed with detailed studies of social behavior in eastern cottontails and swamp rabbits (S. aquaticus). These studies enhanced the behavioral accounts of the three species; however, little was done to determine if the results were consistent with behavior of free-ranging rabbits, to quantify patterns of rabbit activity, or to relate behavior to ecology of the species.

Marsden and Conaway (1963) stated that their enclosure represented a natural, high-density situation, with the only restriction to cottontails being reduced potential for extending home range. However, comparison of several studies indicated physiological and behavioral differences between cottontails confined at high densities and cottontails in natural populations or low-density confined populations (Conaway and Wight, 1962; Casteel, 1966; Marsden and Conaway, 1963). Because conditions created in field enclosures may affect animal behavior directly, information obtained from observation of confined animals may be of limited application to understanding the ecology of free-living animals. In addition, for behavioral information to be most useful, it should be accompanied by descriptions of population characteristics associated with the studied animals.

Variation in activity within leporid species was related to differences in habitat, season, time of day, weather (Vorhies and Taylor, 1933; Orr, 1940; Ingles, 1941; Lechleitner, 1958; Lord, 1964;

Holler and Marsden, 1970), and age, sex, or reproductive condition of individuals (Brambell, 1944; Myers and Poole, 1958, 1962; Marsden and Conaway, 1963; Marsden and Holler, 1964; Trent and Rongstad, 1974). However, in all instances one or two major factors were isolated, and only brief attempts were made to relate activity patterns to the overall ecology of the particular species.

In this study I observed and classified the behavior of free-living Nuttall's cottontails, and evaluated quantitative differences in activity and behavior related to physiological characteristics of leporids and ecological variables. The main objectives of this research were: 1) to compile a descriptive catalog of behaviors, postures, and body movements exhibited by free-living Nuttall's cottontails, 2) to determine and compare attributes of the population of cottontails under study with those reported for Nuttall's cottontails on the same area during the preceeding 8 years, 3) to quantify relationships among activity levels of Nuttall's cottontails and various physiological and environmental variables, and 4) to evaluate quantitatively specific behaviors exhibited by Nuttall's cottontails, in relation to ecology of the species.

## STUDY AREA

Field research was conducted on land managed by U. S. Bureau of Land Management, approximately 5 km W Terrebonne, Deschutes County, Oregon. The 115.7-ha study area was located within 30 km of the western edge of the geographic range of Nuttall's cottontails (Hall, 1981) in the Columbia Basin Physiographic Province (Franklin and Dyrness, 1973). McKay and Verts (1978**b**) stratified the study area into three habitat types, based on topographic, edaphic, and vegetative characteristics. Elevation ranged from 835 to 842 m (McKay and Verts, 1978**b**), and vegetation in this portion of the Juniperus occcidental~~is~~is Zone was most similar to the Juniperus occidentalis/Artemesia tridentata-Purshia tridentata association (Franklin and Dyrness, 1973). Climate was semiarid, with warm to hot dry summers and relatively cold winters. Mean annual precipitation equaled 22.9 cm (U. S. Department of Commerce, 1981).

## METHODS AND MATERIALS

Unbaited wooden box traps (approximately 15 by 19 by 58 cm) were used to capture cottontails. To provide a basis for estimating population attributes, traps were set in a 9- by 13-trap grid with approximately 90 m between traps, and in 1980, were operated 3 consecutive days during alternate weeks in June, 3 consecutive days each week in July, and daily from 1 to 30 August and, in 1981, 3 consecutive days during 3, 3, 2, and 4 weeks in April, May, June, and July, respectively, and daily from 1 to 30 August.

A numbered aluminum eartag was placed in each ear of captured cottontails. Specimens were weighed, and the sex of each cottontail was determined by examination of external genitalia (Petrides, 1951). Age was estimated on the basis of size, pelage, and reproductive status, and juveniles were assigned to specific litter cohorts based on body mass at first capture (McKay and Verts, 1978a). Animals were released at their sites of capture.

Monthly drive censuses were conducted on the study area between September 1980 and March 1981, and in September 1981, to estimate population densities (McKay and Verts, 1978a).

From 25 February through 3 March 1981, livetrapping was conducted in four areas selected as potential sites for systematic behavioral observations. Fifty-eight traps were placed selectively in these areas to locate and mark resident cottontails. Specimens were marked for individual recognition in the field by clipping guard hairs to

form numerals on each side and dyeing the exposed underfur with Nyanzol-D (females) or Rhodamine-B (males).

Between 7 February and 21 July 1981, cottontails were collected to provide an indication of reproductive status of individuals on the study area. Specimens were collected by shooting and trapping in habitats similar to those on the study area, at distances of 0.5 to 8.0 km from the study area. Age, sex, body measurements, and body mass were recorded for each cottontail. Reproductive tracts were examined in a manner similar to that described by Powers and Verts (1971): testes were weighed, stripped of caudae epididymides, and reweighed; female reproductive tracts were examined for presence of spermatozoa, embryos, and implantation sites, fixed in 10% formalin, and preserved in isopropyl alcohol. Ovaries were sectioned and examined in the laboratory for ruptured follicles and corpora lutea.

Ad libitum observations (Altmann, 1974) made during cruises through the study area from June to August 1980 provided valuable information regarding locations of cottontails, effectiveness of different marking techniques and observational methods, and general behavioral patterns and activity levels of cottontails. Cruises were of two types: trapline cruises, consisting of systematic coverage of the entire study area at approximately the same time each day; and selective cruises, during which I covered selected portions of the study area in a nonsystematic manner at various times of day. Date, time, location, and behavior for each sighted cottontail were recorded. Ad libitum observations of cottontail activity also were recorded during cruises in 1981.



In 1981 (March to August), cottontail behavior was observed systematically during periods of 0.75 to 4.00 h duration. Two of the four areas in which cottontails were trapped between 25 February and 3 March 1981 were selected for intensive observation, because of the relatively high densities of cottontails and variety of habitat types thereon, and topography that permitted viewing of relatively large areas from treetops. After observing from several trees in these two areas during March, I selected one area (Area A) and one tree for all subsequent observation periods. Initially, observation periods were scheduled to cover all hours of day and night; however, unsuccessful attempts at observing cottontails in darkness prompted revision of that schedule. After March 1981, observation periods were distributed among hours of daylight and twilight; periods of expected high activity near sunrise and sunset (Lord, 1964; Marsden and Holler, 1964) were sampled more intensively than midday periods.

Observations were made with the aid of 7 by 35 wide-angle binoculars and a Star-tron night scope, from branches of juniper trees approximately 6 m above ground. Careful attention was directed toward remaining relatively silent and motionless during observations periods to minimize the impact of my presence on animal behavior. In addition to the night scope, I used artificial light--a pair of light bulbs (100-watt white or 60-watt red) strung 25 m apart and 5 m above ground between juniper trees, powered by a portable generator--in an attempt to observe nighttime activity of cottontails. This arrangement provided sufficient light; however, noise from the generator was substantial, and probably contributed largely to my failure to observe cottontails by the technique.

Focal-animal sampling (Altmann, 1974) was employed for gathering behavioral data. Whenever possible, time, location, identifying marks, and detailed descriptions of behavior were recorded for observed cottontails. Information was recorded on microcassette tapes and transcribed to field notes. The classification scheme devised by Marsden and Holler (1964) served as a framework for identifying and describing movements, postures, and behavioral patterns exhibited by cottontails.

Ad libitum observations of behavior frequently were conducted in Area A immediately after scheduled observations from tree stands. These cruises of Area A allowed me to confirm my identification of individual cottontails, to locate and identify animals that were present but unobserved during observation periods, and to gather more detailed information about specific cottontails and their behavior.

Site- and time-specific weather data (temperature, percent cloud cover, presence or absence of precipitation, estimated wind speed and direction) 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 U.S. Naval Observatory (1979, 1980).

Densities of cottontail populations were estimated monthly by a modification of the Lincoln index (Bailey, 1952), a maximum likelihood estimator (Edwards and Eberhardt, 1967), or a relative abundance method (McKay and Verts, 1978a). Litter-specific natality

estimates were based on mean litter size for each litter group (Powers and Verts, 1971), estimated numbers of adult females in the population during April, and a constant adult mortality rate during the reproductive season (McKay and Verts, 1978a). Juvenile survival rates for 1980 were estimated from the proportion of estimated numbers born in each litter group that was captured in August (McKay and Verts, 1978a).

Estimated dates of breeding were based on degree of embryonic development for females whose uteri contained visible embryos (Rongstad, 1969), and on presence of spermatozoa in uteri or presence of ruptured follicles or corpora lutea in ovaries for females that did not possess embryos; details of methodology and associated assumptions were described by Powers and Verts (1971). Because estimated peaks of breeding corresponded more closely to a 26-day cycle, I used a 26-day gestation period for calculating dates of breeding for previous pregnancies of females that were pregnant and lactating, rather than the 27-day period used by Powers and Verts (1971).

From the distribution of estimated dates of breeding, I determined dates associated with the production of each of five consecutive litters, or five 26-day reproductive periods, within the 1981 reproductive season. Based on the estimated dates of breeding and the assumption of synchronous breeding that occurs immediately postpartum (Schwartz, 1942; Marsden and Conaway, 1963; Trethewey and Verts, 1971; Powers and Verts, 1971), peaks of breeding were defined as the sixth day of each reproductive period. According to this determination only one instance of breeding among collected females did not occur within

the interval between 3 days before and 4 days following a peak of breeding. For analyses of activity and behavior related to stage of reproduction, I used data from the second through fifth 26-day reproductive periods and from three consecutive postreproductive periods of 26, 26, and 21 days duration. Each reproductive period was further divided into a breeding portion (first 13 days) and a nonbreeding portion (last 13 days) for comparison.

Indices of cottontail activity consisted of: 1) numbers of cottontails observed per hour during observation periods, 2) time cottontails were in view per hour during observation periods, 3) numbers of cottontails sighted per hour during trapline and Area A cruises, and 4) numbers of cottontails captured per night during trapping periods that all traps in the grid were set. Values of these indices were calculated for total samples of cottontails and for different age and sex groups.

Measurements of the following environmental variables were recorded for associated observation periods, cruises, and trapping periods: day of year; reproductive period; day of 26-day reproductive period; time of day (clock time and time relative to sunrise or sunset); number of owls (*Strigidae*) observed per hour; time owls present; time owls active; number of hawks (*Accipitridae*) observed per hour; total number of avian predators observed per hour; number of jackrabbits observed/captured; minimum, maximum, and mean temperatures during the period; minimum and maximum temperatures for the previous day; presence or absence of precipitation during the period and during the previous day; number of consecutive days with and number of

consecutive days without precipitation before the day of the observation; minimum, maximum, and mean cloud cover and wind speed during the period; wind direction; length of the previous night (end of evening civil twilight to beginning of morning civil twilight); duration of lunar illumination during the night; fraction of moon illuminated; time lunar illumination began and ended; phase of moon; and an index to lunar illumination (duration of illumination X fraction of moon illuminated). Not all variables were included in each data set (Appendix, Table A).

Pearson's correlation coefficients were computed for all combinations of activity variables and environmental variables, for the following data sets: 1981 observation periods, 1981 trapline cruises, 1981 Area A cruises, 1980 trapline cruises, 1981 trapping data, and 1980 trapping data. Correlation coefficients were reviewed and relationships were considered in detail for possible biological significance. Data collected during observation periods were subjected to principal component analysis. Five dependent variables (total number of cottontails observed per hour, and numbers of adults, adult males, adult females, and juveniles observed per hour) and nine independent variables (date; time of day relative to sunrise or sunset; number of avian predators observed per hour; mean temperature, cloud cover, and wind speed 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 simple correlation coefficients (Appendix, Table A) and evaluations of potential biological significance. Multiple

regression was used to determine if principal components were related significantly ( $\underline{P} \leq 0.05$ ) to activity.

A catalog of behaviors exhibited by Nuttall's cottontails was compiled. Activity budgets representing relative proportions of time spent engaged in various behaviors were derived solely from systematic observations of cottontail behavior. A generalized activity budget was calculated for the total sample of cottontails and all periods of observation; more specific budgets were calculated for individuals, age and sex groups, and various times of day. Patterns of cottontail behavior were evaluated by computing relative frequencies of previous and subsequent behaviors for each behavioral category.

## RESULTS

Behavioral Catalog

The following is a catalog of behaviors observed in free-living Nuttall's cottontails during cruises and observation periods on the Terrebonne Study Area, between 10 June 1980 and 30 August 1981. Quantitative data listed with descriptions of nine of the behavioral categories and their associated motor patterns were compiled from systematic observations of 1,192 behavioral acts during observation periods; these data correspond to the activity budget for all animals (Table 11). Following each category heading are listed the contribution of that category to total number of behavioral acts observed and to total time cottontails were in view, and the mean duration of all acts within the category. Similar data are listed following headings for motor patterns within each category along with the contribution of that particular motor pattern to number of behavioral acts included in the category and to time spent engaged in acts within the category.

Postures -- Nuttall's cottontails displayed a variety of sitting, standing, and lying postures similar to those reported for other leporids.

Sitting: a stationary, semi-relaxed posture used during resting, feeding and grooming. Alert sitting posture: ears erect, back relatively straight and semi-erect, hind legs under body, front legs vertically straight and planted in front of hind feet. Cottontails sat alertly while feeding (especially in open areas), during grooming

sessions, and when conspecifics or other animals were in the vicinity.

Erect sitting posture: animals sat on hind quarters with body erect; front legs were held limply in front of body, held up to mouth for grooming, or used for balance while feeding on low-hanging juniper foliage. Hunched sitting posture: body compacted into tight ball, back slightly curved, feet and legs under body, head and neck pressed down towards body, ears erect. I interpreted this posture to be related to heat conservation as during cold mornings cottontails frequently hunched on rock outcrops or bare soil in sunlight.

Lying: relaxed resting posture; belly on ground with front legs under chest and hind legs bent and at sides, head held up and ears erect. Concealment posture: a modified lying posture, with body stretched longitudinally and compressed dorso-ventrally against the ground, head and neck stretched forward and flat against the ground, ears laid back against body [same posture was noted among snowshoe hares (Lepus americanus; Grange, 1932), black-tailed jackrabbits (Lechleitner, 1958), and desert cottontails (Sylvilagus audubonii; Ingles, 1941)]. Concealment posture was exhibited by some cottontails that "froze" as I approached at close distances, and by some specimens immediately after release from live-traps. These observations supported Ingles (1941) statement that the posture was used as a predator avoidance mechanism. The concealment posture was similar to submissive posture described by Marsden and Holler (1964), but was never observed during social interactions.

Loafing: a posture similar to lying but more relaxed; body stretched on ground, with belly or side against soil surface, front



and hind legs extended, head and ears held semi-erect; animals appeared "sprawled out" (similar to descriptions provided by Marsden and Holler, 1964; Ingles, 1941; Grange, 1932). Cottontails were observed to lie and to loaf in shaded areas during late morning hours on hot days; similarly, Ingles (1941) observed desert cottontails to loaf on cool, moist lawns or on freshly cultivated fields during hot days. I interpreted these postures to be related to thermoregulation; the postures should facilitate conductive cooling by increasing the surface area of pelage in contact with soil cooler than surrounding air.

Standing: an erect, bipedal posture; hind feet spread apart, hind legs extended vertically, back straight and nearly vertical, front legs hanging limply or used for support and balance. Cottontails stood during feeding to obtain seed heads from cheatgrass (Bromus tectorum) and to forage on low-hanging juniper foliage. Grange (1932) described similar use of the standing posture by snowshoe hares for feeding on twigs and buds. Exploring cottontails sometimes stood upright seemingly to increase their fields of view while conducting visual searches; likewise, jackrabbits reportedly stood to investigate their surroundings when alarmed from a distance (Lechleitner, 1958).

Body Movements -- The following list includes some of the movements exhibited by Nuttall's cottontails; these movements generally occurred rapidly, were brief in duration, and usually occurred in association with one or more of the behaviors described later in the catalog.

Shake: vigorous shaking of the entire body. Cottontails sometimes shook immediately after dusting, or during a grooming

session. Head shake: shaking of head and ears only; occurred during grooming, feeding, and resting, apparently in response to immediate irritation by fleas, ticks, or flies. Ear twitch: rapid movement of ears in response to irritation by pests; observed during feeding, resting, grooming. Stretch: stretching of legs and body. Complexity of stretching varied from extending a front leg while sitting, to more involved stretches of the entire body. During whole-body stretches, cottontails first elevated their rumps by fully extending their hind legs vertically while the front feet remained on the ground; they then arched their backs and simultaneously extended their heads, necks, and front legs forward. Stretching was observed most frequently following long periods of resting, and accompanied grooming on some occasions. Wave: sudden waving of front paws up and down in quick, alternating motions while sitting in an erect sitting posture. Although this behavior was observed in eastern cottontails, swamp rabbits (Marsden and Holler, 1964), black-tailed jackrabbits (Lechleitner, 1958), and snowshoe hares (Severaid, 1942), its significance remains unknown. In this study, waving was observed three times among two adult female cottontails. On one occasion waves were interspersed with grooming; during the other instances waving was preceded by motionless sitting and was followed by face rubbing. Search: movements of head, neck, and upper body that suggested cottontails were actively searching for something. Typically from an erect sitting posture or sometimes from a standing posture, cottontails swung their heads from side to side, moved their ears in various directions, and sometimes sniffed

vigorously at the air or ground. Cottontails searched during exploring, investigation, and sometimes after being flushed from cover. The latter instances represent times when I assumed a motionless stance immediately after flushing animals; the cottontails seemed to be looking for the source of disturbance. Lunge: On two occasions I observed cottontails approach, then lunge at low hanging juniper twigs. The animals charged at twigs and crashed into them with their chin, neck, and chest areas, then backed up short distances and repeated the act as many as three times. This behavior seemed to be somewhat like chinping, described by Marsden and Holler (1964) for swamp rabbits, and perhaps served to transfer odoriferous material from chin glands of cottontails onto objects.

Nonsocial Behavior -- Seven of nine categories of nonsocial behavior included behavioral acts observed during observations periods, and accounted for 92.8% of the total number of behavioral acts observed and 92.6% of the total time cottontails were in view.

Feed (25.4% of total number, 58.5% of total time, mean duration = 7.27 min): ingestion of food plus activities associated with obtaining food. When possible, feeding was categorized according to the food item being consumed (grass, forb, shrub, juniper) and the intensity of activity (low, moderate, high). During low-intensity, or interrupted feeding, ingestion of food frequently was interrupted to sit and chew, to sit motionless in an alert posture, or to move amongst food sources (such interruptions usually accounted for 20-50% of feeding time). Moderate-intensity, or causal feeding, included

movements amongst food items and short interruptions to move slightly, shift position, or sit motionless (noningestive activities accounted for <20% of feeding time). High-intensity feeding was characterized by nearly continuous activity, generally in one spot; cottontails occasionally sat alertly for brief periods (1 to 5 s) between mouthfuls of forage.

Grasses were the most commonly eaten food item, representing 72% of all feeding bouts (Table 1), and nearly 80% of total feeding time; cheatgrass, needlegrass (Stipa thurberiana), and squirreltail (Sitanion hystrix) were abundant on the study area, and constituted a large percentage of the grass eaten by cottontails. Cottontails consumed flowers of green rabbitbrush (Chrysothamnus viscidiflorus) on three occasions, but were not observed to feed on other available shrub species (gray rabbitbrush, Chrysothamnus nauseosus; bitterbrush, Purshia tridentata; currant, Ribes sp.; big sagebrush, Artemisia tridentata). Juniper foliage was eaten during 8% of all feeding bouts (Table 1); however, cottontails did not use juniper in months other than July and August. During July and August, juniper was eaten during 12.4% of all feeding bouts, and constituted 11.1% of total feeding time. Cottontails were not observed to eat forbs, probably because of low abundance of forbs on the area during 1981 and my difficulty in identifying forbs from great distances. Forb consumption likely constituted a small portion of the unknown food categories.

Table 1. Items fed upon, and time and frequency of feeding on each, by Nuttall's cottontails during observation periods on the Terrebonne Study Area, Deschutes County, Oregon, March-August 1981.

Food Category	Intensity of feeding Activity <sup>a</sup>	% of Feeding Bouts	% of Feeding Time	Mean Duration of bouts (min)
Grass	Unknown	3.6	3.1	6.2
Grass	Low	7.9	6.6	6.0
Grass	Moderate	47.5	46.1	7.0
Grass	High	13.2	23.6	13.0
Grass	All	(72.2)	(79.4)	(8.0)
Shrub	Moderate	0.3	0.1	3.0
Shrub	High	0.7	0.2	2.0
Shrub	All	(1.0)	(0.3)	(2.3)
Juniper	Low	0.3	0.2	5.0
Juniper	Moderate	1.7	0.8	3.5
Juniper	High	5.9	5.0	6.2
Juniper	All	(7.9)	(6.0)	(5.6)
Unknown	All	(18.8)	(14.3)	(5.5)

<sup>a</sup> Intensity of feeding activity: low = noningestive activities associated with feeding accounted for 20-50% of feeding time; medium = noningestive activities comprised < 20% of feeding time; high = nearly continuous ingestion of food.

Cottontails gained access to cheatgrass seed heads by standing erect and by climbing onto nearby rocks. As a third method of obtaining seed heads, animals grabbed the bases or midportions of stems with their mouths, then slid the stems through their mouths until the seed heads were reached. While feeding on bunchgrasses, cottontails sometimes gnawed and pulled vigorously with their mouths at material around the bases of these plants.

Rest (13.7% of total number, 23.0% of total time, mean duration = 5.30 min): maintenance of a relatively motionless posture, categorized according to the posture of the resting animal. Possible functions of resting may include: thermoregulation (warming or cooling), aid to digestion, energy conservation through reduced metabolism, concealment from predators, or response to local environmental disturbance. Nuttall's cottontails used forms and crevices in rock outcrops when they rested. Orr (1940) speculated that Nuttall's cottontails living in areas with dense sagebrush made use of forms for protection during resting periods. McKay and Verts (1978b) suggested that Nuttall's cottontails on the Terrebonne Study Area used forms much less frequently than crevices and fissures in rock outcrops for daytime retreats, because of sparse, shrubby vegetation on the area. During cruises conducted between February and August 1981, 78 of 630 (12%) cottontails sightings were of animals that flushed from forms or sat on forms at the time of sighting. During the same period, I observed only seven cottontails to enter or exit crevices in rock outcrops; four of these observations occurred during cruises and three occurred during observation periods. During

December 1980 and January 1981, when snow covered the ground, I observed cottontail tracks that led to and from rock outcrops. I believe that cottontails made extensive use of such crevices, especially during periods of extreme cold or heat, but that use of these refuges was extremely difficult to detect. Sitting (13.3% of total number, 21.1% of total time, mean duration = 5.03 min; 96.9% of resting bouts, 92.1% of resting time): cottontails sat motionless in either the alert or hunched posture. Lying (0.1% of total number, 1.6% of total time, duration = 60.00 min; 0.6% of resting bouts, 6.9% of resting time): cottontails rested in a relaxed lying posture. Lying was observed only once during observation periods; a juvenile male rested in a lying posture under a juniper sapling for 60 min, beginning 62 min before sunset on 25 August 1981. Loafing (0.3% of total number, 0.2% of total time, mean duration = 2.08 min; 2.5% of resting bouts, 1.0% of resting time): on four occasions during observation periods, an adult female (F79) rested in a sprawled loafing posture; each time loafing immediately followed dusting. Cottontails also were observed lying (n = 18) and loafing (n = 4) during my cruises.

Locomote (38.5% of total number, 6.3% of total time, mean duration = 0.52 min): movement from one location to another. Locomotory acts were categorized according to their apparent function. Simple transport (35.2% of total number, 4.3% of total time, mean duration = 0.39 min; 91.5% of locomotory acts, 69.5% of locomote time): movements to get from one place to another; assumed when no definite stimuli for movement were apparent. Movements in this category were

classified further according to the speed at which they occurred: rapid, or running speed (27.4% of simple transport movements, 25.1% of all locomotory acts, mean duration = 0.14 min); moderate speed (44.8% of simple transport movements, 40.9% of all locomotory acts, mean duration = 0.29 min); slow, or hopping speed (27.9% of simple transport movements, 25.5% of all locomotory acts, mean duration = 0.82 min). Explore (2.3% of total number, 1.2% of total time, mean duration = 1.68 min; 5.9% of locomotory acts, 18.6% of locomote time): investigative or searching behavior; cottontails appeared alert, active, and intent while exploring. Use of senses was apparent; vigorous sniffing of air and ground, frequent visual searching, and conspicuous ear movements were common components of exploring. Reproductive exploring (85.2% of exploring acts) consisted of intense searching activity by cottontails during reproductive periods, and was classified as such only if an adult female was observed in the area where the exploring took place during the same observation period. In these instances exploring animals (60.9% adults males, 39.1% unmarked or unidentified adults) presumably were searching for receptive females. On five occasions during peaks of reproductive activity, I observed two or more cottontails exploring simultaneously within the home range of an adult female. When cottontails exhibited exploring-type behavior within 2 m of a conspecific, behaviors were classified as social interactions (following or investigation). Environmental exploring (14.8% of exploring acts) consisted of cottontails investigating physical features of their environment. For example, an adult female was observed to explore a large crevice in



the lava rocks on an open ridgeslope, and a juvenile was seen to explore a site under a juniper tree that was visited recently by a conspecific. Wander (0.8% of total number, 0.7% of total time, mean duration = 2.88 min; 2.0 % of locomotory acts, 11.8% of locomote time): erratic, seemingly aimless or uncertain movement through an area, characterized by frequent changes in speed and direction; similar to exploring behavior, but lacking the distinct "searching" elements of exploring. Eight of nine instances involved wandering by juveniles; this behavior may be related to the animals being in relatively unfamiliar areas inhabited by conspecifics. The other instance of wandering consisted of erratic movement of an adult female within her home range. Escape and concealment (0.3% of total number, <0.1% of total time, mean duration = 0.06 min; 0.7% of locomotary acts, 0.1% of locomote time): evasive movement in response to environmental disturbance (noise from aircraft, chipmunk (Tamias amoenus) alarm calls, humans walking through area). Typically, cottontails moved rapidly to nearby cover then sat motionless. Escape and concealment activities resulting from encounters with predators were categorized as interspecific interactions.

Groom (8.1% of total number, 1.6% of total time, mean duration = 0.61 min): cleaning or caring for the body. Grooming occurred as a brief act, interrupting some other activity, seemingly the result of immediate irritation to the body; as a grooming session of significant duration, generally involving a combination of different grooming acts; during social interactions, possibly in preparation for parturition, lactation, or nest-building among females or to improve

sexual attractiveness among males; or as displacement activity, during encounters with conspecifics or with a human observer.

Grooming activities were categorized according to methods of grooming described by Marsden and Holler (1964); many of these patterns also were observed among snowshoe hares (Grange, 1932).

Scratching with hind foot (2.7% of total number, 0.1% of total time, mean duration = 0.08 min; 33.0% grooming bouts, 4.4% of total grooming time): from a sitting posture, cottontails leaned to one side, put their weight on one of the hind quarters, then used the opposite hind leg to scratch; scratching usually was directed at the back of the head, ears, neck, or shoulders, but occasionally was directed at the face and eyes. Licking or picking at the body with mouth and tongue (1.5% of total number, 0.2% of total time, mean duration = 0.50 min; 18.6% of grooming bouts, 15.1% of total grooming time): cottontails contorted their bodies into a variety of positions to enable them to lick or pick at portions of the chest, abdomen, back, rump, hind legs, and front legs. Some of the common positions were: sitting back on rump, back arched, neck stretched forward and downward to reach chest and abdomen; sitting on rump, a hind leg fully extended forward, for picking at thigh and lower leg; leaning to one side, stretching laterally to reach side, back, rump and hind leg; sitting erect, holding front legs and paws up to mouth for cleaning. Grooming face with front paws (0.5% of total number, 0.1% of total time, mean duration = 0.40 min; 6.2% of grooming bouts, 4.0% of grooming time): cottontails typically sat in erect sitting posture and rubbed their faces with front paws. During observation periods, face rubbing was

observed six times as a single grooming act and six times within combinations of grooming acts. Face rubbing by adult males ( $n = 2$ ) occurred while males attended females, and included interspersed rubbing of front paws together under the chin. Perhaps this process was related to olfactory communication, and served to transfer odoriferous materials from chin gland onto face. Mykytowycz (1968) reported that secretions from anal, inguinal, and submandibular glands of European wild rabbits served to communicate information about age, sex, reproductive condition, and group membership. Rubbing of paws under the chin did not accompany face rubbing in adult females ( $n = 8$ ) or juvenile males ( $n = 2$ ). Biting and cleaning feet with mouth and tongue (0.1% of total number, <0.1% of total time, mean duration = 0.78 min; 1.0% of grooming acts, 1.3% of grooming time): cottontails sat on their rumps, shifted their weight to one side, extended a hind leg forward, bent forward and picked at foot with mouth; the animals cleaned the tops of their feet, between the toes, and the undersides of the feet. This behavior was observed only twice during observation periods, but was seen six more times during cruises.

Combinations of grooming methods (2.4% of total number, 1.2% of total time, mean duration = 1.50 min; 30.0% of grooming acts, 73.4% of grooming time): observed combinations of grooming methods included: scratching and licking (65.5% of combinations, 21.6% of grooming bouts, 31.1% of grooming time); licking and face rubbing (17.2% of combinations, 5.7% of grooming bouts, 7.6% of grooming time); licking and biting (3.4% of combinations, 1.1% of grooming bouts, 9.3% of grooming time); scratching, licking, and biting (10.3% of

combinations, 3.4% of grooming bouts, 15.3% of grooming time); scratching, licking, biting, and face rubbing (3.4% of combinations, 1.1% of grooming bouts, 10.1% of grooming time). Dusting (0.8% of total number, <0.1% of total time, mean duration = 0.06 min; 9.3% of grooming acts, 0.9% of grooming time): rapid, dog-like rolling in loose soil (same as descriptions by Marsden and Holler, 1964, and Grange, 1932), typically in an open, sandy spot near cover. Dusting was observed nine times among adult females during observation periods.

Tree-climbing activities (3.9% of total number, 3.0% of total time, mean duration = 2.43 min): Nuttall's cottontails climbed and performed various activities in juniper trees. Since 1968, several investigators observed Nuttall's cottontails in juniper trees in central Oregon (Verts et al., in press). Between June 1980 and August 1981, I observed 17 instances of tree-climbing, involving at least nine different cottontails. Of these instances, 8 occurred during observation periods in 1981, and represented 47 acts included as tree-climbing activities. Apparently, arboreal activities of lagomorphs were not reported heretofore. Move (2.0% of total number, 0.1% of total time, mean duration = 0.14 min; 51.1% of tree-climbing activities, 3.0% of time spent in trees): cottontails moved about on branches and trunks of juniper trees. Typically, cottontails climbed in deformed trees that had sloping or nearly horizontal boles that afforded access to upper branches of the trees. Movement onto and off of trees usually was rapid, and generally was followed or preceded by a period during which the animal sat motionless in the tree. When in

trees, cottontails moved about on branches as small as 2.5 cm in diameter, and as high as 3 m above ground; however, they were not particularly graceful as they moved. Sit (1.1% of total number, 1.6% of total time, mean duration = 4.53 min; 27.7% of tree-climbing activities, 51.5% of time spent in trees): cottontails sat relatively motionless on branches or trunks of juniper trees. The high percentage of time spent sitting seemed to reflect a relatively high degree of cautiousness among animals while they were in trees. Such cautiousness would be warranted, possibly because of increased exposure to predators, and decreased ability to escape. Feed (0.8% of total number, 1.4% of total time, mean duration = 5.77 min; 19.1% of tree-climbing activities, 45.4% of time spent in trees): while in trees, cottontails generally fed amongst relatively dense clumps of foliage from an erect sitting or standing posture. When standing, cottontails fully extended their hind legs, used their front legs for balance, and stretched their necks to obtain foliage or to lick droplets of water from the foliage. Groom (0.1% of total number, <0.1% of total time, mean duration = 0.07 min; 2.1% of tree-climbing activities, 0.1% of time spent in trees): one cottontail was observed to groom while sitting in a juniper tree; the very brief grooming act interrupted a period of motionless sitting, and appeared to occur in response to an immediate irritation to the body.

Interspecific interactions (1.3% of total number, 0.2% of total time, mean duration = 0.50 min): Nuttall's cottontails were observed to interact with individuals of other species on 15 occasions during observation periods. Encounters with predators: nine encounters

between cottontails and avian predators [eight with great horned owls (Bubo virginianus), and one with a red-tailed hawk (Buteo jamaicensis)] accounted for 59.0% of time spent interacting with other animals. During three of these encounters, predators merely flew overhead without attempting to capture animals, and cottontails responded by moving rapidly to nearby cover. However, on the remaining six occasions predators made definite attempts to capture cottontails. In all but one instance cottontails avoided capture, by quickly moving to cover. The other animal also avoided capture, but only after enduring a 4-min "face-off" with a great horned owl that landed 3 m from the cottontail under low-hanging branches of a large juniper tree. The owl stood motionless and watched the adult female cottontail from the opposite side of a barrier of dead branches, as the cottontail "nervously" pranced about, before dashing 15 m to cover. During cruises through the study area I observed five instances of predators (two coyotes [Canis latrans], a red-tailed hawk, a juvenile golden eagle [Aquila chrysaetos], and an unidentified falcon) feeding on cottontails. Interactions with nonpredators: . 40.9% of time spent interacting with other animals consisted of four encounters with California ground squirrels (Spermophilus beechyii) and two encounters with black-tailed jackrabbits (Lepus californicus). All encounters with California ground squirrels consisted of squirrels aggressively chasing cottontails, and cottontails rapidly retreating to cover. No physical contact was observed between squirrels and cottontails , although squirrels got within 1 m of cottontails during several chases. One observation of a cottontail-jackrabbit

interaction involved an adult female cottontail aggressively chasing a jackrabbit out of her home range. During the other cottontail-jackrabbit encounter, a juvenile cottontail sat motionless and watched as a jackrabbit wandered by within 1 m, then followed the jackrabbit approximately 20 m before the jackrabbit disappeared from view. On four occasions during cottontail reproductive periods, jackrabbits wandered through the area and exhibited exploring-type behavior; three times jackrabbits appeared to actively pursue cottontails, as they moved along behind cottontails engaged in reproductive following. Jackrabbits also were observed in close proximity to socially interacting cottontails on two occasions during cruises through the study area. No physical contact was observed between cottontails and jackrabbits. Cottontails exhibited no observable response to yellow pine chipmunks (Tamias amoenus) that occasionally passed within 1 m while cottontails were feeding.

Transitional acts (1.9% of total number, <0.1% of total time, mean duration = 0.08 min): brief body movements or spurts of activity that occurred between major behavioral acts; examples included: stretching, shaking, standing, changing orientation or posture, head shake, ear twitch, single hop, hop up onto or down from rock, kick out with hind legs, and wave.

Coprophagy: no definite occurrences of Nuttall's cottontails ingesting their fecal material were observed during observation periods. However, I believe that this behavior probably occurred during some grooming sessions, and was undetected merely because of difficulty in distinguishing it from grooming at great distances.

During cruises I observed cottontails to ingest their feces on four occasions. Further evidence of coprophagy was found upon examination of stomach contents from collected cottontails; 26 of 67 stomachs contained fecal pellets.

Vocalizations: unlike eastern cottontails and swamp rabbits, that reportedly produced three and five distinct vocalizations, respectively (Marsden and Holler, 1964), Nuttall's cottontails emitted only two distinct sounds. The distress cry described by Marsden and Holler (1964) and a quiet, repititious chirping-type sound ("ft-ft"; possibly same as chirp described by Marsden and Holler, 1964) were emitted by cottontails removed from live traps. No vocalizations were heard among free-ranging cottontails.

Social Behavior -- Behaviors that involved two or more individuals responding to the actions of each other accounted for only 7.1% of the total number of behavioral acts observed and 7.4% of the total time cottontails were in view. Many of the social interactions I observed were similar to descriptions presented by Marsden and Holler (1964); therefore, I used large portions of their classification scheme as a framework for categorizing social behavior of Nuttall's cottontails.

Reproductive interactions (6.5% of total number, 6.9% of total time, mean duration = 3.39 min, 90.6% of social interactions, 94.6% of time spent engaged in social interactions): interactions that occurred among adult cottontails during reproductive periods.

Following (75.3% of reproductive interactions, 87.4% of time spent in reproductive interactions, mean duration = 3.78 min): maintenance of close proximity (typically  $\leq 2$  m) to a female by a male; often



consisted of interspersed pursuit of moving females (designated as "following" by Marsden and Holler, 1964) and passive attendance of stationary females by males (designated as "consort" by Marsden and Holler, 1964). Likely some following episodes constituted reproductive chases (Marsden and Holler, 1964); however, I could not distinguish these instances because I did not have precise knowledge of the reproductive status of participating females. Avoidance (9.1% of reproductive interactions, 2.2% of time spent in reproductive interactions, mean duration = 0.84 min): evasive movement in response to an approaching conspecific. Avoidance was included as a reproductive interaction (unlike its categorization by Marsden and Holler, 1964) because in five of seven instances, adult females moved to avoid approaching males during reproductive periods. One instance involved mutual avoidance between a male and a female after a coincidental encounter; and in one instance a juvenile avoided a nearby adult female after being chased by her. Male-male interactions (5.2% of reproductive interactions, 3.8% of time spent in reproductive interactions, mean duration = 2.46 min): on two occasions exploring males were observed to approach other males; in both situations one male moved in an investigative manner, to within 1 m of a second male, and the second male responded by moving a short distance and continuing with its exploring. No physical contact was observed between males. These observations were similar to those reported for black-tailed jackrabbits (Lechleitner, 1958) and desert cottontails (Ingles, 1941); in wild populations of both species, males were generally tolerant of each other, and fighting was not observed.

Within confined populations of eastern cottontails and swamp rabbits, attempts to bite and kick occurred during competition for receptive females and during aggressive chases, but fighting was not part of normal social activity (Marsden and Holler, 1964). In contrast, vigorous fighting was observed among male snowshoe hares in captivity (Grange, 1932), and among male eastern cottontails during experiments conducted in small artificial test arenas (Brenner and Flemming, 1979). Further investigation is needed to determine if differences in aggressiveness and tolerance are related mainly to confinement of individuals or to genuine ethological and ecological differences among species. Other (2.6% of reproductive interactions, 1.5% of time spent in reproductive interactions, mean duration = 2.00 min): on one occasion a male and female cottontail exhibited several additional sex-specific behaviors and reproductive interactions described by Marsden and Holler (1964). The 2-min episode proceeded as follows: exploring male moved towards female ("approach"); female rapidly moved several meters, then wheeled to face male ("threat," "facing-off"); male moved rapidly towards female ("rush"); female responded by jumping over male ("jump"); male chased female for 30 s ("reproductive chase"); both animals stopped at cover, female 1 m in front of male. No copulations, attempted mounts by males, or presentations by females were observed.

Nonreproductive interactions (0.7% of total number, 0.4% of total time, mean duration = 1.88 min; 9.4% of social interactions, 5.4% of time spent in social interactions): interactions among adults and juveniles, plus adult interactions occurring outside of the breeding

season. Investigation (25.0% of nonreproductive interactions, 13.3% of time spent in nonreproductive interaction, mean duration = 1.00 min): investigative, exploring-type behavior directed at a conspecific at close range (<2 m). A juvenile was observed to approach and investigate a feeding adult female. Aggressive chase (75.0% of nonreproductive interactions, 86.7% of time spent in nonreproductive interaction, mean duration = 2.50 min): on three occasions adult females chased juveniles after being approached by them. Although distance between animals was sometimes less than 1 m, no physical contact was observed during chases. Interactions between adult females and juveniles were much less intense than the extremely aggressive, and sometimes fatal, encounters reported to occur between adult female and juvenile European rabbits (Mykytowycz and Dudzinski, 1972; Southern, 1948).

#### Attributes of the Population

General trends in population density of cottontails on the study area during the course of this study (Fig. 1) were similar to those that occurred during 8 preceeding years on the same area (Skalski and Verts, 1981; Hundertmark, in litt.), and reflected reproductive cycles of cottontails and mortality patterns. Increase in density between April and July 1980 coincided with production of at least four litter groups, and juvenile survival rates (Table 2) typical of the 8 preceeding years (Hundertmark, 1982).

Estimated overwinter survival of 65% (from August 1980 to April 1981) corresponded to relatively mild temperatures and absence of deep snow on the area (Table 3), and provided for a relatively large

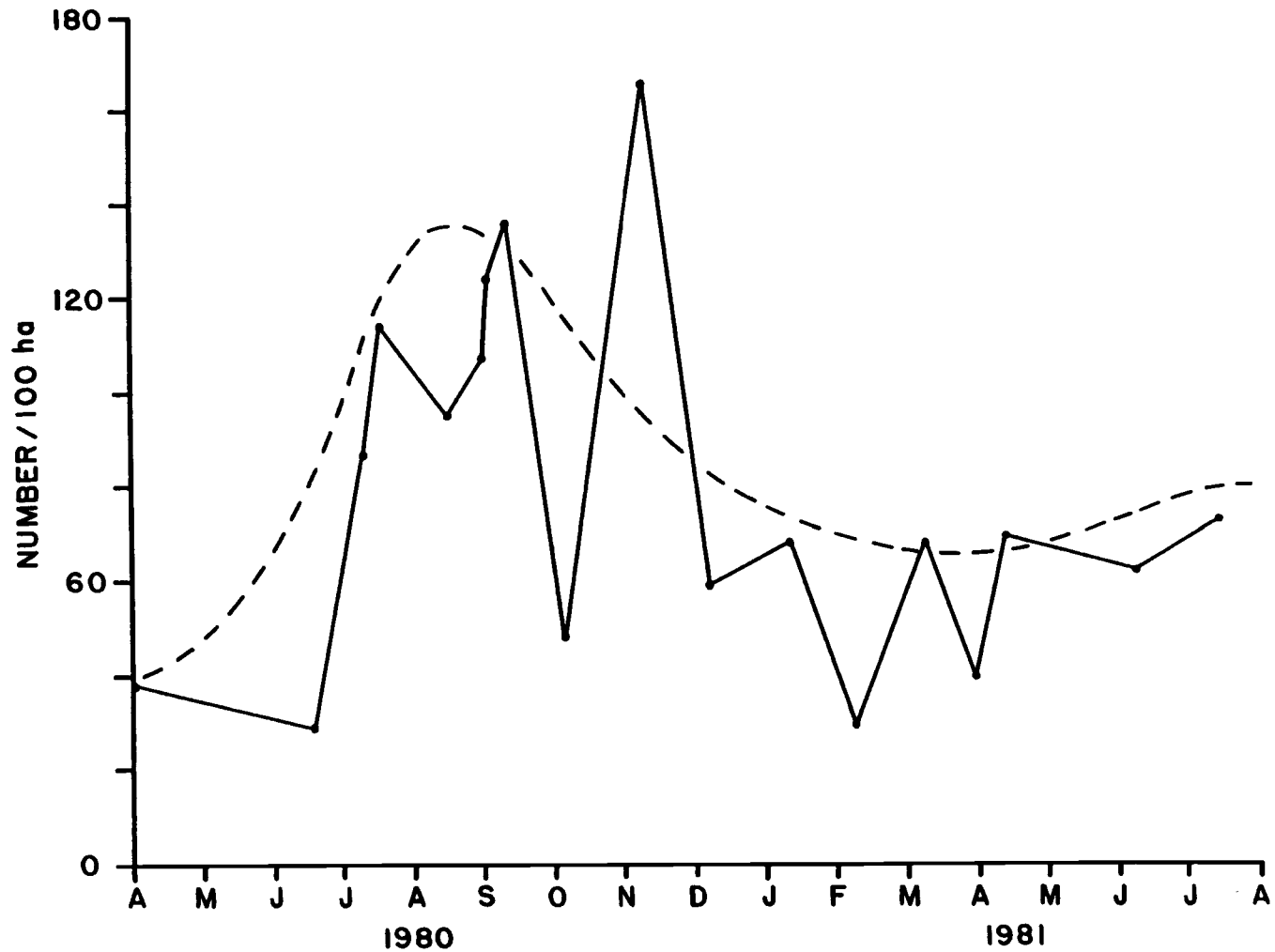


Figure 1. Estimates of population density for Nuttall's cottontails on the Terrebonne Study Area, Deschutes County, Oregon, April 1980-August 1981. April 1980 estimate from Hundertmark (1982). Dashed line represents estimated trend in density, with adjustments for low estimates induced by inclement weather and high estimates induced by unseasonably high temperatures.

Table 2. Estimates of litter-specific natality and survival, and numbers of juveniles captured from each litter group, for Nuttall's cottontails on the Terrebonne Study Area, Deschutes County, Oregon, 1980-1981.

Year	Litter <sup>a</sup> Group	Estimated Number Born	Percent Estimated Survival <sup>b</sup>	Juveniles Captured	
				Number	% of Estimated Number Born
1980	1	90	9	10	11
	2	107	19	16	15
	3	90	38	21	23
	4	63	19	9	14
	All	350	21	56	16
1981	1	168	-	21	13
	2	204	-	8	4
	3	175	-	5	3
	4	123	-	3	2
	All	670	-	37	6

<sup>a</sup> Evidence for some breeding during a fifth period in both years.

<sup>b</sup> From birth to 31 August each year.

Table 3. Monthly weather information from Redmond FAA AP weather station, Deschutes County, Oregon, June 1980-August 1981.<sup>a</sup>

Month	Total Precipitation (cm)	% of Average Monthly Precipitation <sup>b</sup>	Maximum depth of snow on ground (cm)	Mean Temperature (°C)	Deviation from Average Mean Monthly Temperature (°C) <sup>b/</sup>
June 1980	3.40	131	0	12.9	-1.7
July 1980	0.48	61	0	19.5	+0.8
August 1980	T	0	0	16.4	-1.3
September 1980	1.65	162	0	14.9	+0.6
October 1980	1.83	100	0	9.1	0.0
November 1980	2.34	79	2.54	4.6	+0.7
December 1980	1.83	61	5.08	3.6	+2.8
January 1981	1.83	59	5.08	0.3	+1.3
February 1981	1.65	90	2.54	2.9	+0.8
March 1981	1.73	126	Trace	4.3	+0.6
April 1981	1.22	117	Trace	7.3	+0.4
May 1981	3.25	132	0	10.0	-0.7
June 1981	1.17	45	0	14.1	-0.5
July 1981	0.33	42	0	17.5	-1.2
August 1981	0.00	0	0	20.4	+2.7

<sup>a</sup> U. S. Department of Commerce (1980, 1981)

<sup>b</sup> 30-year average, 1941-1970

breeding population in 1981. Estimates of dates of breeding for adult female cottontails collected during 1981 suggested the occurrence of four periods of extensive breeding and a fifth period during which scattered breeding took place (Fig. 2). Separation of captured juveniles into litter groups, based on body mass (Fig. 3), supported this breeding chronology.

Despite apparently significant production of offspring (Table 2), subsequent estimates of density (Fig. 1) and field observations did not indicate a large increase in population size from April to July 1981. Juvenile survival rates could not be calculated because of low numbers of juvenile captures during August 1981.

Area A was selected for behavioral observations because trapping suggested a relatively high concentration of cottontails; therefore, densities on this portion of the study area were probably greater than those of the entire study area. A minimum of 19 cottontails (number of identifiable individuals captured or observed) used Area A between 24 February and 30 August 1981. Even if all 12 adults observed in Area A were assumed to be residents, the resultant density of approximately 2 adults/ha was considerably lower than the 6.9 to 28.4 adult cottontails/ha estimated for penned populations observed by Marsden and Conaway (1963), Marsden and Holler (1964), and Sorensen et al. (1972). In addition, the density of cottontails on Area A only slightly exceeded the maximum estimated density for the entire study area during the period 1972 through 1979 (Skalski and Verts, 1981).

Because estimates of population attributes did not differ greatly from those reported for Nuttall's cottontails on the same area during

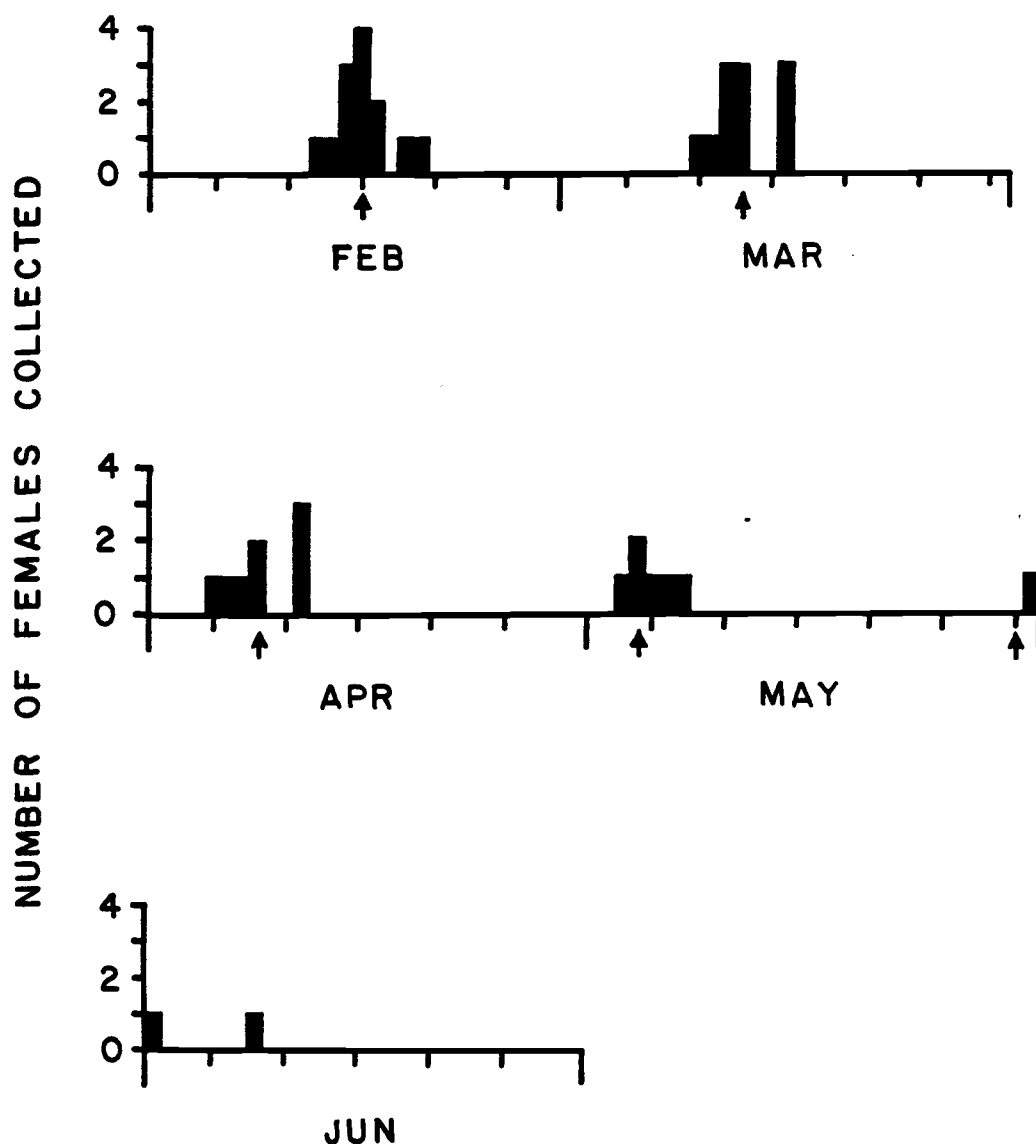


Figure 2. Estimated dates of breeding for female Nuttall's cottontails collected in Deschutes County, Oregon, February-July 1981. Two dates were computed for females that were pregnant and lactating, except for the female that gave birth on 8 June. Arrows indicate estimated peaks of breeding based on a 26-day gestation period and immediate postpartum estrus (Marsden and Conaway, 1963; Trethewey and Verts, 1971; Powers and Verts, 1971).



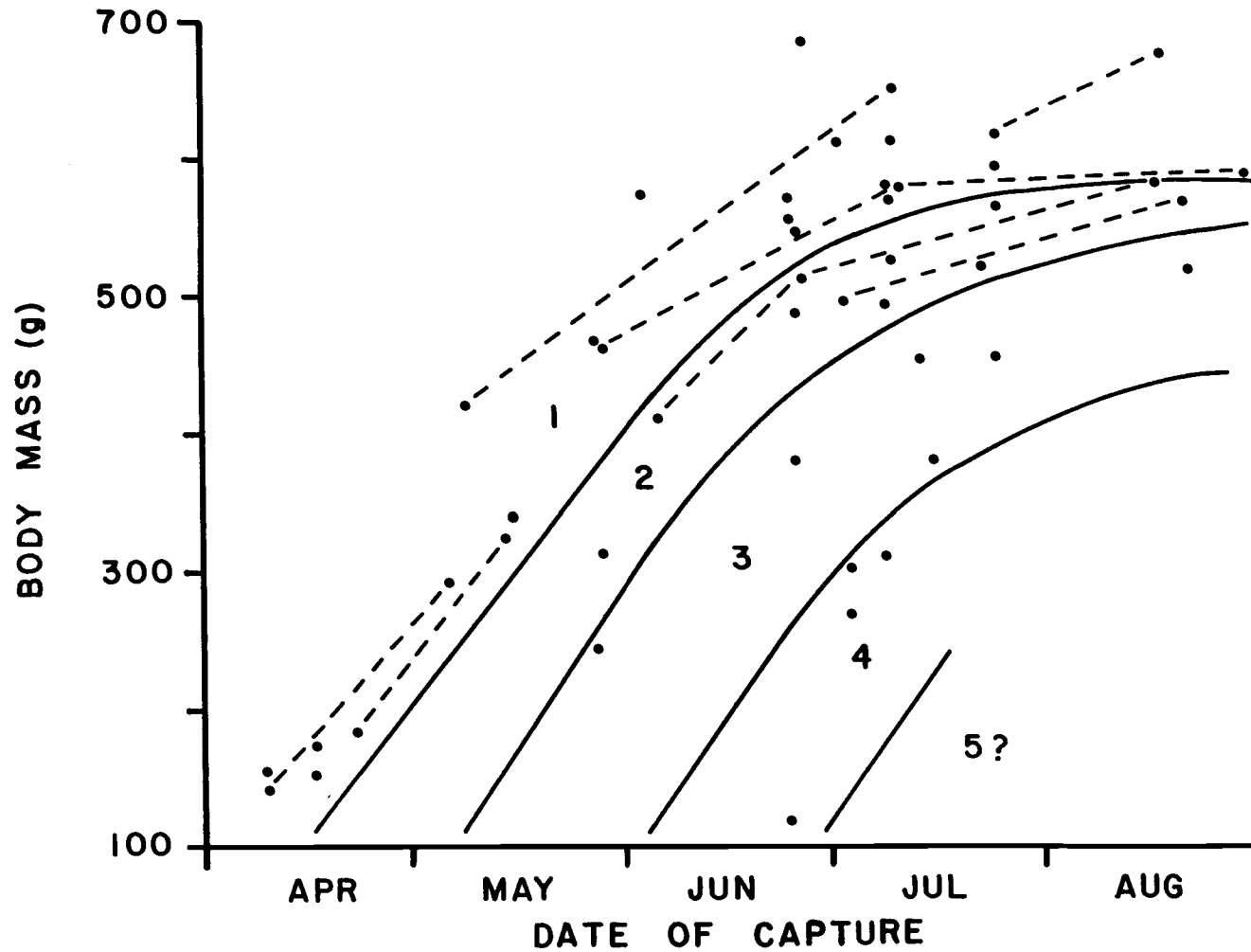


Figure 3. Separation of juvenile Nuttall's cottontails captured in 1981 on the Terrebonne Study Area, Deschutes County, Oregon, into litter groups, based on body mass. Dashed lines connect body masses of recaptured individuals.

the preceeding 8 years, behavioral and ecological implications of this research should have general applicability to Nuttall's cottontails in this region.

#### Activity Patterns

No single environmental factor or group of factors emerged as a significant determinant of cottontail activity levels. Many of the activity-environment relationships analyzed were not significantly correlated ( $P < 0.05$ ) and those that were correlated significantly generally had low  $r$  values (Appendix, Table A). Some  $r$  values were low probably because of nonlinear relationships or complex interactions involving more than two variables. Furthermore, relationships that had moderate  $r$  values generally could be explained in terms of phenomena that had little significance to rabbit ecology. Principal component analysis performed on the nine selected environmental variables resulted in the creation of three components that explained 70% of the variation in environmental variables (Table 4). I interpreted the first component to be 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 component to be representative of daily influences (time of day, temperature, wind speed), and the third component possibly to be representative of astronomical phenomena (length of night, lunar illumination). Multiple regression of the principal components on indices of cottontail activity did not explain large proportions of the variation in activity; however, the presence of significant relationships ( $P < 0.05$ ) suggested several trends.

Table 4. Component correlations and proportions of variation explained, for principal components created from nine selected environmental variables that were measured for observation periods on the Terrebonne Study Area, Deschutes County, Oregon, March-August 1981.

Variable <sup>a</sup>	Component		
	1	2	3
DATE	0.52	0.02	0.15
RTIME	0.09	0.60	-0.18
AVIANPH	-0.37	0.13	-0.13
MEANT	0.39	0.45	-0.13
PRECIP	0.34	0.09	0.58
MEANCC	-0.33	0.19	-0.19
MEANW	-0.12	0.57	0.01
NIGHT	-0.37	0.11	0.55
ILLUM	-0.24	0.20	0.49
Variation explained	0.35	0.20	0.15
Cumulative variation explained	0.35	0.55	0.70

<sup>a</sup> DATE = day of year, RTIME = time of day relative to sunrise or sunset, AVIANPH = number of avian predators observed per hour, MEANT = mean ambient temperature during the period, PRECIP = number of consecutive days without precipitation before the day of observation, MEANCC = mean cloud cover during the period, MEANW = mean wind speed during the period, NIGHT = length of previous night (or current night, for nighttime observation periods), ILLUM = index to lunar illumination = time of illumination X fraction of moon illuminated).

Activity of adult males was most strongly influenced by the seasonal component ( $R^2 = 0.11$ ), whereas activity of adult females was related to the component representative of daily influences ( $R^2 = 0.04$ ). Juvenile activity was related to the seasonal component ( $R^2 = 0.22$ ) and the astronomical component (cumulative  $R^2 = 0.35$ ); however, the strength of these relationships may be largely an artifact of seasonal increase in numbers of juveniles present on the study area.

Seasonal Activity -- Activity levels of adult males and adult females were more similar during the reproductive season than during the postreproductive season; activity of both sexes increased from the second through fourth reproductive periods then declined during the fifth, less pronounced reproductive period (Tables 5 and 6, Fig. 4). No consistent pattern of activity was evident between breeding and nonbreeding portions of reproductive periods, among males or females (Fig. 5).

No adult males were observed during observation periods after mid-May (Fig. 4), and numbers of sightings (Table 5) and captures (Table 6) indicated that activity of adult males decreased dramatically after May. The decline in activity of adult males corresponded with regression of testes among males collected nearby (Table 7), and suggested that males were responsible for cessation of breeding in 1981.

Activity levels of adult females were much more stable than those of adult males throughout the course of the study; this stability resulted in activity levels of adult females that generally were more than twice those of adult males during the postreproductive season (Tables 5 and 6, Fig. 4).

Table 5. Numbers of marked Nuttall's cottontails sighted per 10 h of cruising, on the Terrebonne Study Area, Deschutes County, Oregon, March-August 1981.<sup>a</sup>

Month	Cruising Time (h)	Number sighted/ 10 h of cruising		
		Adult Male	Adult Female	Juvenile
March	17.1	3.5	5.2	0.0
April	9.3	13.9	12.9	4.4
May	13.9	8.6	18.7	6.5
June	11.4	3.5	14.9	8.8
July	18.1	0.0	12.7	13.8
August	15.7	0.0	9.6	11.5
<hr/>				
April	48.6	2.5	3.1	0.0
May	44.7	1.8	3.1	3.6
June	33.4	0.3	1.8	2.7
July	59.0	0.7	2.4	4.1
August	97.0	0.8	2.5	7.1

<sup>a</sup> Upper portion of table represents cruises in Area A, lower portion represents cruises on traplines.

Table 6. Numbers of Nuttall's cottontails captured per 1000 trap-nights, on the Terrebonne Study Area, Deschutes County, Oregon, February-August 1981.

	Number Trap-nights	Number of captures/1000 trap-nights			
		Adult Male	Adult Female	Juvenile Male	Juvenile Female
25-28 February <sup>a</sup>	232	125.0	86.2	0.0	0.0
1-27 March <sup>a</sup>	348	63.2	60.4	0.0	0.0
9-24 April	1053	20.9	6.6	1.9	2.8
6-29 May	1053	8.5	7.6	3.8	3.8
3-26 June	702	2.8	5.7	9.1	8.6
1-24 July	1434	2.1	4.2	9.8	6.9
1-30 August	3510	0.3	0.6	1.7	0.0

<sup>a</sup> Represents selective trapping conducted on four areas that supported relatively high concentrations of cottontails.

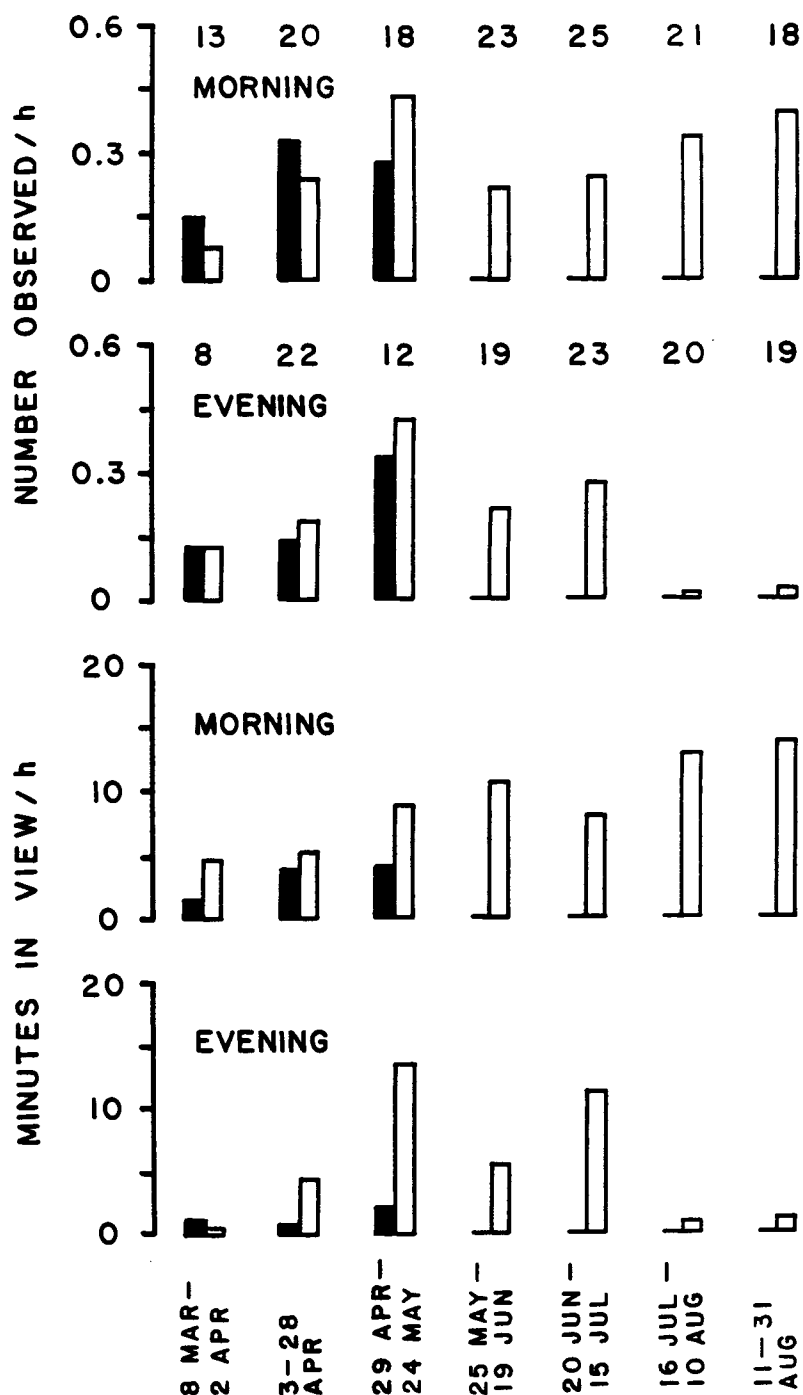


Figure 4. Activity of adult Nuttall's cottontails during morning (sunrise - 1 h to sunrise + 3h) and evening (sunset - 2 h to sunset + 1h) observation periods, related to stage of reproduction. First four periods along abscissa represent the second through fifth reproductive periods of 1981; remaining three periods represent portions of the postreproductive season. Solid bars represent males, open bars represent females. Numbers above bars indicate approximate hours of observation.

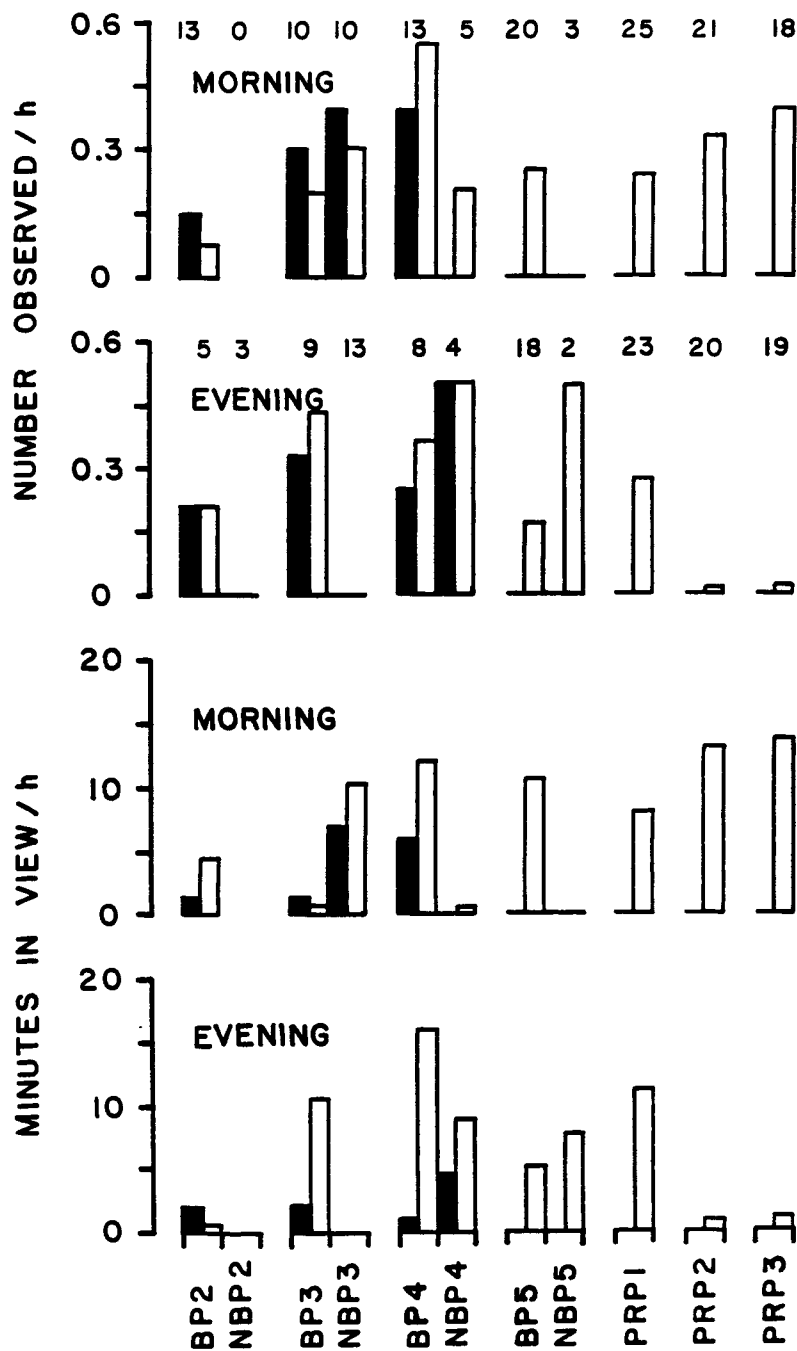


Figure 5. Activity of adult Nuttall's cottontails during morning (sunrise -1 h to sunset + 3 h) and evening (sunset -2 h to sunset + 1 h) observation periods, related to stage of reproduction, with each 26-day reproductive period divided into 13-day breeding (BP) and nonbreeding (NBP) portions. Solid bars represent males, open bars represent females. Reproductive and postreproductive periods (PRP) are same as those in Fig. 4. Numbers above bars indicate approximate hours of observation.



Table 7. Testes weights for adult<sup>a</sup> male Nuttall's cottontails collected between 7 February and 2 July 1981, Deschutes County, Oregon.

Collection Number	Date Collected	Weight of testis without epididymides (g)		
		Left	Right	Average
001	7 Feb	3.9	3.1	3.5
002	7 Feb	3.6	3.3	3.5
003	14 Feb	5.9	6.2	6.1
004	14 Feb	5.4	4.8	5.1
005	14 Feb	5.0	4.9	5.0
015	24 Mar	6.0	6.5	6.3
020	8 Apr	-	5.6	5.6
021	8 Apr	6.5	6.4	6.5
022	8 Apr	5.2	5.5	5.4
023	8 Apr	6.5	6.8	6.7
028	6 May	4.5	3.9	4.2
031	13 May	5.4	5.6	5.5
037	7 June	0.8	1.0	0.9
042	25 June	0.6	0.6	0.6
046	2 July	0.5	0.5	0.5

<sup>a</sup> based on ossification of epiphyseal cartilage (Hale, 1949).

All indices showed an increase in juvenile activity through July (Tables 5 and 6); however, these indices may be misleading because all litter groups were considered together, and increasing density of juveniles likely influenced levels of activity indices. In general, juveniles of a particular litter group became observable about 1 month after the estimated peak of birth for that litter group (Table 8), then exhibited an increase and peak of activity within the next 1 to 2 months of life (Tables 9 and 10). Subsequent decline in juvenile activity (Tables 9 and 10) likely was related to decreased numbers of juveniles on the study area and to increased wariness of surviving juveniles.

Daily Activity. — Cottontails exhibited a bimodal pattern of daytime activity, with peaks in the early morning after sunrise and in early evening near sunset (Figs. 6 and 7); all age and sex cohorts exhibited similar patterns. After the morning peak, cottontail activity declined gradually, and reached a minimum between 4 h after sunrise and 2 h before sunset (Figs. 6 and 7).

#### Activity Budget

Feeding was the most common activity, representing nearly 60% of the time cottontails were in view (Table 11). Cottontails fed almost exclusively on grasses during the spring and early summer, but included juniper in their diets during July and August (Table 12). Percentage of time spent feeding was highest during the hour before sunrise and the hour after sunset (Table 13), and feeding was associated strongly with locomotory acts (Tables 14 and 15).

Table 8. Estimated peaks and ranges of dates of birth, and dates of first capture, dates of first sighting, and numbers of captured individuals and subsequent sightings of them, for juveniles of 1981 litter groups, Terrebonne Study Area, Deschutes County, Oregon.

Litter Group	Estimated dates of births <sup>a</sup>		Date of first Capture	Number of individuals captured	Date of first sighting	Number of sightings
	Peak	Range				
1	13 March	10-16 March	6 April	21	9 April	43
2	8 April	5-11 April	8 May	8	8 May	22
3	4 May	3-7 May	27 May	5	5 June	15
4	30 May	30 May-8 June	24 June	3	3 July	9
5?	25 June	25 June-3 July	-	1	-	-

<sup>a</sup> Based on Fig. 2.

Table 9. Numbers of juvenile Nuttall's cottontails captured per 1000 trap-nights, by litter group, on the Terrebonne Study Area, Deschutes County, Oregon, April-July 1981.

Month	Number Trap-nights	Number captures/1000 trap-nights			
		1	2	3	4
April	1053	4.7	-	-	-
May	1053	5.7	1.9	0.9	-
June	702	8.5	4.3	1.4	1.4
July	1434	7.7	3.5	3.5	2.1

Table 10. Numbers of marked juvenile Nuttall's cottontail sightings per 10 h of cruising<sup>a</sup>, by litter group, on the Terrebonne Study Area, Deschutes County, Oregon, April-August 1981.

Month	Cruising Time (h)	Number sightings/10 h			
		1	2	3	4
April	57.4	0.3	-	-	-
May	46.5	1.9	1.1	-	-
June	36.3	0.3	2.2	0.6	-
July	61.6	1.0	0.3	1.5	0.7
August	106.7	2.3	0.7	0.4	0.5

<sup>a</sup> Includes cruises along traplines and those made in selected areas.

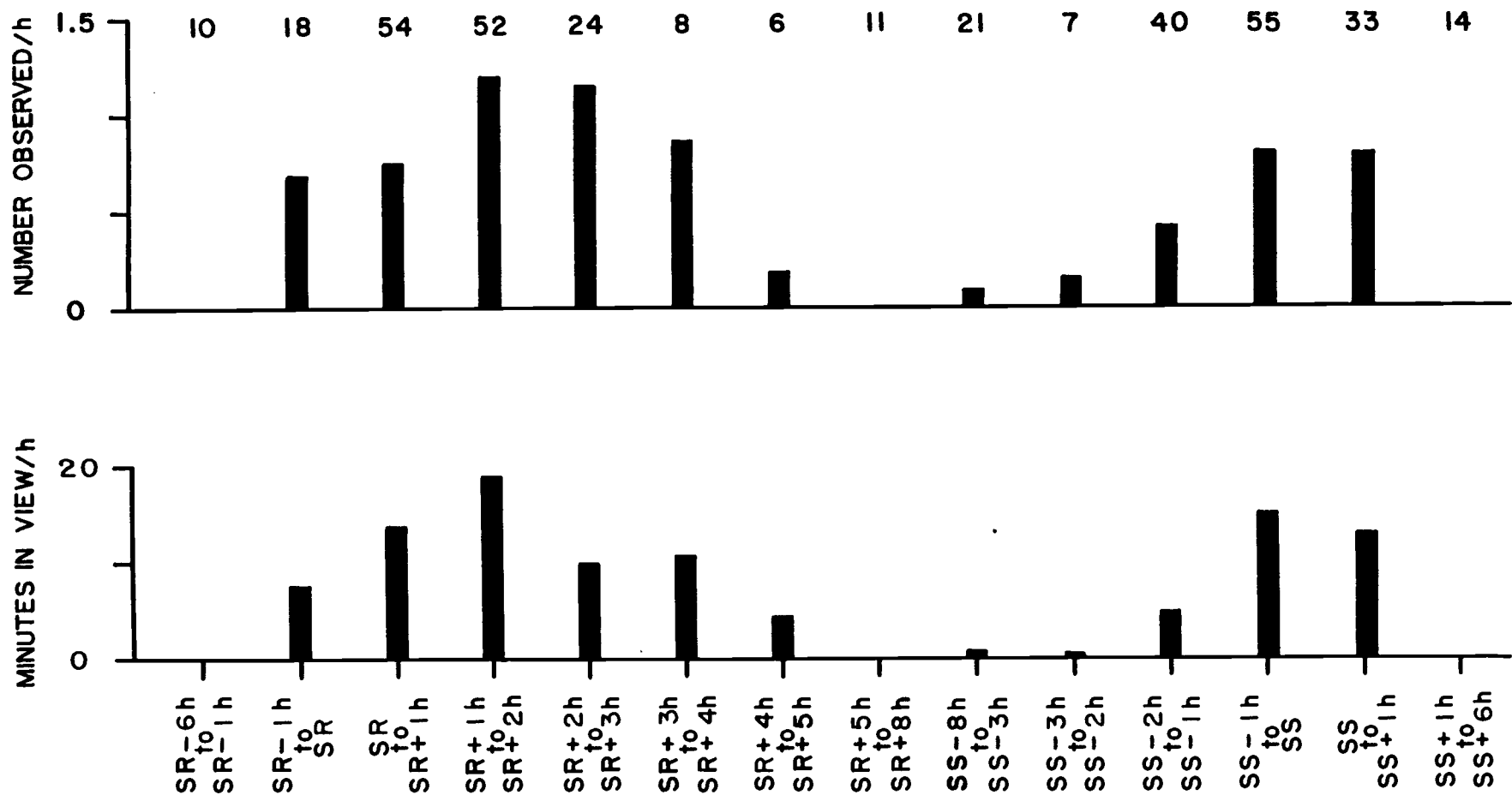


Figure 6. Numbers of Nuttall's cottontails observed per hour and minutes cottontails were in view per hour, related to time of day in relation to sunrise (SR) and sunset (SS), during observation periods on the Terrebonne Study Area, Deschutes County, Oregon, March-August, 1981. Numbers along top of figure indicate approximate hours of observation for each interval.

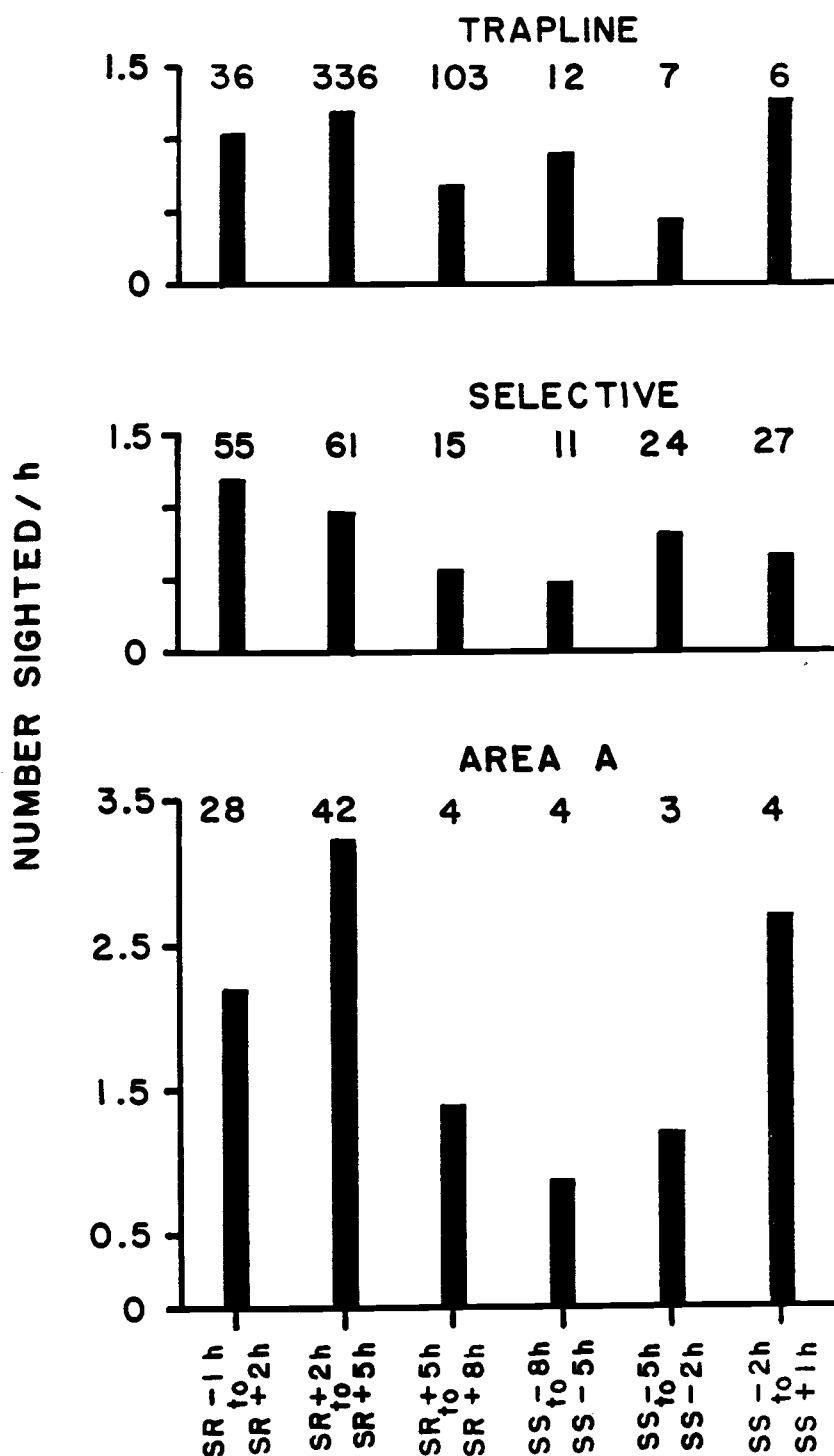


Figure 7. Numbers of Nuttall's cottontails sighted per hour of cruising, related to time of day in relation to sunrise (SR) and sunset (SS), Terrebonne Study Area, Deschutes County, Oregon, June-August 1980 and February-August 1981. Numbers along top of each graph indicate approximate hours spent cruising during each interval.

Table 11. Summary of activity of Nuttall's cottontails in Area A of the Terrebonne Study Area, Deschutes County, Oregon, 1981.

Animal <sup>a</sup>	Applicable Period	Number of Captures	Number of Sightings During Cruises	Number of Observation Periods	Total Time in View (h)	% of time in view							
						Feed	Rest	Locomote	Groom	Tree-climb	Inter-specific Inter-actions	Transitional Acts	Social Inter-actions
F79	26 Feb-29 Aug	2	32	28	15.5	75.3	14.8	4.7	1.5	0.2	0.1	<0.1	3.5
F23	25 Feb-12 Aug	5	38	15	10.0	60.2	26.9	2.7	1.2	-	0.7	0.1	8.3
F87	2 Mar-29 Aug	1	49	17	7.7	51.8	16.1	3.9	3.7	23.4	<0.1	0.1	0.9
F41	25 Feb- 5 July	3	14	2	0.1	-	-	45.8	-	-	-	-	54.2
M82	27 Feb- 8 May	2	15	10	2.2	21.7	25.0	23.3	6.4	-	0.1	0.2	23.3
M60	26 Feb- 6 June	2	26	4	0.5	13.5	1.4	8.0	-	-	-	-	77.1
M59	26 Feb-12 May	6	3	2	0.4	-	-	9.1	-	-	-	-	90.9
JM1	24 July-30 Aug	2	18	6	6.9	63.6	31.0	4.5	0.8	-	-	0.1	-
JM3	13 July-29 Aug	1	22	20	13.5	67.4	26.8	4.2	0.9	-	<0.1	0.1	0.5
All F <sup>b</sup>	25 Feb-29 Aug	11	143	-	34.2	63.3	19.9	4.0	1.9	5.4	0.2	<0.1	5.3
All M <sup>c</sup>	26 Feb- 8 June	15	47	-	3.9	14.7	15.1	17.2	3.7	-	0.1	0.1	49.0
All JM	13 July-30 Aug	3	40	-	20.4	66.2	28.2	4.3	0.9	-	<0.1	0.1	0.3
All A <sup>d</sup>	25 Feb-29 Aug	26	212	-	40.4	55.6	20.4	6.1	2.0	4.6	0.2	<0.1	11.1
All J <sup>e</sup>	14 Apr-30 Aug	3	78	-	22.4	63.7	27.5	6.8	0.9	0.3	0.2	<0.1	0.6
All	25 Feb-30 Aug	29	290	-	62.7	58.5	23.0	6.3	1.6	3.0	0.2	<0.1	7.4

<sup>a</sup> F = adult female, M = adult male, JM = juvenile male, A = adult, J = juvenile, unmarked animals were classified as adults or juveniles based on their size and general appearance.

<sup>b</sup> Includes 10 sightings and 0.95 h observation time of unidentified adult females during 7 observation periods.

<sup>c</sup> Includes 5 captures of 3 adult males not observed during observation periods, plus 1 sighting and 0.80 h observation time of unidentified adult males during 9 observation periods.

<sup>d</sup> Includes information for all unidentified adult males and females, plus 22 sightings and 2.25 h observation time unidentified or unmarked adults during 19 observation periods.

<sup>e</sup> Includes 38 sightings and 1.94 h observation time of unmarked juveniles during 5 observation periods.



Table 12. Seasonal distributions of occurrences and of time in view for behaviors exhibited by Nuttall's cottontails during observation periods, Terrebonne Study Area, Deschutes County, Oregon, 1981.<sup>a</sup>

Behavior	% of time in view (% of behavioral acts observed)						
	RP2	RP3	RP4	RP5	PRP1	PRP2	PRP3
	n=43 t=1.7h	n=110 t=5.4h	n=144 t=8.4h	n=73 t=7.2h	n=208 t=10.2h	n=306 t=14.4h	n=308 t=15.5h
Feed	2 (2)	47 (16)	31 (14)	81 (33)	67 (26)	59 (26)	65 (32)
Grass	2 (2)	33 (9)	17 (6)	75 (27)	55 (20)	46 (12)	54 (26)
Juniper	0 (0)	0 (0)	0 (0)	0 (0)	2 (1)	8 (4)	6 (3)
Rest	37 (9)	25 (12)	29 (15)	15 (12)	20 (16)	24 (14)	22 (13)
Locomote	28 (54)	6 (33)	5 (37)	2 (36)	8 (41)	6 (35)	5 (40)
Groom	3 (5)	3 (9)	<1 (3)	1 (8)	2 (12)	3 (9)	1 (7)
Tree-climb	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	8 (11)	5 (4)
Interspecific interactions	0 (0)	0 (0)	1 (4)	<1 (4)	<1 (2)	<1 (<1)	0 (0)
Transitional acts	<1 (2)	<1 (2)	<1 (4)	<1 (1)	0 (0)	<1 (1)	<1 (1)
Social interactions	30 (28)	19 (28)	34 (23)	1 (5)	<1 (1)	0 (0)	1 (1)
Reproductive	30 (28)	19 (28)	32 (20)	0 (0)	0 (0)	0 (0)	0 (0)
Non-reproductive	0 (0)	0 (0)	2 (3)	1 (5)	<1 (1)	0 (0)	1 (1)

<sup>a</sup> Seasonal distributions according to stage of reproduction: RP = reproductive periods within 1981 breeding season, PRP = post-reproductive periods following 1981 breeding season, RP2 = 8 March-2 April, RP3 = 3 April-28 April, RP4 = 29 April-24 May, RP5 = 25 May-19 June, PRP1 = 20 June-15 July, PRP2 = 16 July-10 August, PRP3 = 11 August-31 August.

Table 13. Distribution of time rabbits were in view during observation periods, among behavioral categories and among time intervals related to sunrise and sunset, for Nuttall's cottontails on the Terrebonne Study Area, Deschutes County, Oregon, March-August 1981.

Interval <sup>a</sup>	% Total Observation Time <sup>b</sup>	% Total Time Rabbits in View <sup>c</sup>	% of Time rabbits in view within interval <sup>d</sup>							
			Feed	Rest	Locomote	Groom	Tree-climb	Inter-specific Inter-actions	Transitional Acts	Social Inter-actions
SR-1h to SR	5.0	3.4	65.0	29.1	5.8	-	-	-	0.1	-
SR to SR+1h	15.3	20.4	56.4	18.1	6.2	1.1	13.5	<0.1	<0.1	4.8
SR+1h to SR+2h	14.7	27.2	61.3	16.4	7.4	1.8	0.5	<0.1	<0.1	12.6
SR+2h to SR+3h	6.7	7.0	57.0	14.3	14.1	5.3	-	1.0	0.1	8.3
SR+3h to SR+4h	2.3	2.2	9.4	63.5	17.2	4.7	4.7	0.2	<0.1	0.2
SR+4h to SR+8h	4.7	0.6	T	-	T	-	-	-	-	-
(SR-1h to SR+8h)	(48.7)	(60.8)	(57.8)	(19.0)	(8.0)	(1.9)	(4.9)	(0.1)	(<0.1)	(8.2)
SS-8h to SS-2h	7.9	0.2	-	T	T	-	-	-	T	-
SS-2h to SS-1h	11.4	4.9	55.5	34.3	9.4	0.6	-	-	-	0.1
SS-1h to SS	15.6	22.7	51.9	34.6	3.1	1.5	-	0.5	<0.1	8.3
SS to SS+1h	9.4	11.4	77.3	16.0	2.3	0.2	-	-	0.1	4.1
(SS-8h to SS+1h)	(44.3)	(39.3)	(59.6)	(29.3)	(3.7)	(1.0)	(0.0)	(0.3)	(0.1)	(6.0)

<sup>a</sup> SR = sunrise, SS = sunset; intervals in parentheses represent sums for 9-hour intervals of daylight related to sunrise and sunset.

<sup>b</sup> observation time = time spent observing from elevated platform = 352 h

<sup>c</sup> time rabbits in view =  $\Sigma$  (number rabbits in view x time in view) = 62.7 h

<sup>d</sup> T = value omitted because interval represents less than 1.0% of total time rabbits were in view.

Table 14. Behavioral patterns observed<sup>a</sup> among Nuttall's cottontails during observation periods, Terrebonne Study Area, Deschutes County, Oregon, March-August 1981.

Behavior	Adjusted Frequency of Occurrence (%) of Previous Behaviors <sup>b</sup>							
	Feed	Rest	Locomote	Groom	Tree-climb	Inter-specific Inter-actions	Transitional Acts	Social Inter-actions
Feed	15.7	18.7	56.5	6.1	0.4	-	1.7	0.9
Rest	22.1	1.4	47.9	20.0	-	2.1	4.3	2.1
Locomote	52.4	19.3	5.8	17.1	1.8	0.4	1.8	1.5
Groom	20.5	38.6	33.0	2.3	-	-	5.7	-
Tree-climb	66.6*	-	33.3	-	-	-	-	-
Interspecific Interactions	50.0	33.3	-	-	-	16.7	-	-
Transitional acts	14.3	61.9	9.5	9.5	-	-	-	4.8
Social interactions	16.7	23.3	30.0	-	-	-	-	30.0

<sup>a</sup> Each table value represents the percentage of occurrences of a behavior listed in the left-handed column that were preceeded by a behavior listed in the box head.

<sup>b</sup> Adjusted by excluding instances for which previous behavior was unknown.

\* Represents instances that cottontails were feeding on juniper from the ground before they climbed onto a juniper tree.

Table 15. Behavioral patterns observed<sup>a</sup> among Nuttall's cottontails during observation periods, Terrebonne Study Area, Deschutes County, Oregon, March-August 1981.

Behavior	Adjusted Frequency of Occurrence (%) of Subsequent Behaviors <sup>b</sup>							
	Feed	Rest	Locomote	Groom	Tree-climb	Inter-specific Inter-actions	Transitional Acts	Social Inter-actions
Feed	15.2	12.8	60.1	7.4	0.8	0.4	1.2	2.1
Rest	28.1	1.3	34.6	22.9	-	0.7	7.8	4.6
Locomote	51.8	25.7	6.8	10.8	0.4	-	0.8	3.6
Groom	15.1	30.1	50.5	2.2	-	-	2.2	-
Tree-climb	17.0*	-	83.0	-	-	-	-	-
Interspecific Interactions	-	77.8	22.2	-	-	-	-	-
Transitional acts	19.0	33.3	23.8	23.8	-	-	-	-
Social interactions	10.5	15.8	26.3	-	-	-	5.3	42.1

<sup>a</sup> Each table value represents the percentage of occurrences of a behavior listed in the left-handed column that were followed by a behavior listed in the box head.

<sup>b</sup> Adjusted by excluding instances for which subsequent behavior was unknown.

\* Represents instances that cottontails left trees but continued to feed on same trees from ground.

Nuttall's cottontails were observed to climb in juniper trees on 15 occasions during July and August 1981 (Table 12). Observations suggested that tree-climbing was conducted largely to consume juniper foliage or water droplets on the foliage; 55.9% of time in trees was spent feeding on juniper, and occurrences of tree-climbing were associated strongly with periods of feeding on juniper from the ground (Tables 14 and 15). Tree-climbing occurred during morning hours, especially during the hour after sunrise, when cottontails observed in July and August spent nearly 20% of their time in trees (Table 16).

Resting was the second-most time-consuming behavior exhibited by cottontails (Table 11), and was relatively uniformly interspersed among locomotory, feeding, and grooming activities (Tables 14 and 15). Percentage of time spent resting was greatest during the hour before sunrise and during the interval from 3 h after sunrise to sunset (Table 13).

Locomotion and grooming, essential to the functioning, maintenance, and survival of animals accounted for a relatively small portion of the time budget of Nuttall's cottontails (Table 11). Variation in proportion of time spent moving indicated that cottontails reduced their movement during periods of increased feeding, resting, and social interaction (Table 13). Similarly, grooming appeared to be a relatively low-priority activity, conducted for brief periods at relatively regular intervals, but occurring most frequently during periods of reduced feeding and resting (Table 13).

Rate of daytime interaction between cottontails and predators seemed low. A pair of great horned owls that nested in Area A

Table 16. Relationship between tree-climbing activity of Nuttall's cottontails on the Terrebonne Study Area, Deschutes County, Oregon, and time of day, July-August, 1981.

Category	Time Interval <sup>a</sup>						
	SR-1h to SR	SR to SR+1h	SR+1h to SR+4h	SR+4h to SR+8h	SS-8h to SS-2h	SS-2h to SS	SS to SS+1h
Time spent observing from tree stand (h)	9.8	22.0	21.7	3.7	6.1	39.0	11.8
Time cottontails in view <sup>b</sup> (h)	2.1	9.3	10.9	0.0	0.0	9.5	4.0
Percent time in trees	0.0	18.3	1.8	0.0	0.0	0.0	0.0
<hr/>							
Time spent cruising (h)	3.7	5.7	104.0	7.0	6.7	2.3	3.8
Number cottontails sighted/h	0.8	1.6	2.3	0.9	1.0	0.9	0.5
Number cottontails seen in trees	0	1	4	2	0	0	0

<sup>a</sup> SR = sunrise, SS = sunset

<sup>b</sup>  $\Sigma$  (number cottontails in view x time in view)

accounted for eight of only nine encounters between cottontails and predators during 62.9 h of observed cottontail activity; the remaining encounter involved a red-tailed hawk. In no instance did a predator capture a cottontail. In addition, only five instances of predators feeding on cottontails were observed during almost 800 h of cruising on the study area during 1980 and 1981. These data suggested that predation was not the most critical factor related to survival of Nuttall's cottontails on the study area during spring and summer. During observation periods, all encounters between cottontails and owls occurred between 38 min before sunset and 8 min after sunset; the encounter with a hawk occurred during the second hour after sunrise. Immediately before encounters with predators, all observable cottontails either were feeding or resting (Tables 14 and 15).

Overall, social behavior accounted for a relatively small portion of the activity budget of Nuttall's cottontails (Table 11); however, occurrence of social interactions varied considerably with season (Table 12), and adult cottontails interacted socially only during the reproductive season. Cottontails interacted socially during most daylight hours in which they were observed; however, the proportion of time spent engaged in social behaviors was greatest during the second and third hours after sunrise and during the hour before sunset (Table 13). Because of these trends, and the paucity of observations of reproductive behaviors other than following, I speculated that much of the social behavior of Nuttall's cottontails occurred during nighttime. Social interactions were associated strongly with locomotion (Tables 14 and 15). Social behavior of juvenile cottontails consisted

entirely of nonreproductive interactions with adult females, and typically involved investigation by the juveniles and a subsequent aggressive chase of the juvenile by the adult.



## DISCUSSION

Leporid species exhibit varying degrees of sociality: European rabbits live colonially in underground burrows and interact frequently with one another (Mykytowycz, 1968); eastern cottontails are typically solitary in their habits and interact with conspecifics only during the breeding season (Marsden and Holler, 1964); swamp rabbits display variations of some of the strong social characteristics of European rabbits (Marsden and Holler, 1964), and could be classified as moderately social. In this study, adult Nuttall's cottontails interacted socially only during the reproductive season, and social interactions occurred with less frequency and intensity than those reported for eastern cottontails and swamp rabbits (Marsden and Holler, 1964). These findings corroborate Orr's (1940) statement that Nuttall's cottontails were more solitary in their habits than other members of the genus Sylvilagus.

Studies of birds (Lack, 1968), primates (Crook, 1970), and ungulates (Jarman, 1974) showed that social structures adopted by populations of various species were related closely to ecological factors. The Terrebonne Study Area lies in a semiarid region near the periphery of the range of Nuttall's cottontails. Unpredictable moisture availability (Skalski and Verts, 1981:332, Fig. 4) may be related to the solitary lifestyle adopted by Nuttall's cottontails in this area during the nonreproductive season. Dispersion of cottontails throughout suitable habitat distributed relatively uniformly on the study area (McKay and Verts, 1978**b**) may reduce

intraspecific competition and facilitate optimum forage (i.e. moisture) availability. This would be especially beneficial during dry summer months when forage abundance and moisture availability are lowest (Hundertmark, 1982), and moisture requirements of lactating females and growing young are greatest (Richards, 1979).

Nevertheless, no single environmental factor exhibited a dominating influence on cottontail activity patterns. Similar results were obtained in studies of activity patterns of rodents (O'Farrell, 1974; Blaustein and Fugle, 1981). Instead, results from this study suggested that seasonal and daily activity levels of Nuttall's cottontails may be determined by complex interrelationships among reproductive condition, temperature and moisture requirements of animals, and combinations of environmental constraints to which cottontails are subjected.

Seasonal activity patterns and behavior of adult Nuttall's cottontails seemed to be related more strongly to stage of reproduction than to environmental conditions. Occurrence of adult social behavior only during the reproductive season was consistent with findings of increased social activity related to onset of the reproductive season for European rabbits (Brambell, 1944; Myers and Mykytowycz, 1958; Myers and Poole, 1958, 1962), black-tailed jackrabbits (Lechleitner, 1958), eastern cottontails (Marsden and Conaway, 1963; Marsden and Holler, 1964), and swamp rabbits (Marsden and Holler, 1964). In addition, there was evidence for decreased activity related to declining reproductive condition of males and cessation of breeding among Nuttall's cottontails. Powers and Verts

(1971) reported that paired-testes weights greater than 2.0 g corresponded to copious amounts of testicular spermatozoa and indicated male fertility among Nuttall's cottontails. No male collected in June 1968 or June 1969 had an average weight of paired testes that was less than 2.0 g; in 1969, the mean of average weights of paired testes did not fall below 2.0 g until August (Powers and Verts, 1971). However, in 1981 all adult males collected after 13 May exhibited average weights of paired testes less than 1.0 g, and presumably were infertile. Although data are scanty, I believe that the sample of males was representative of males on the study area, and that only a few scattered males remained reproductively active. These males accomplished the limited breeding that occurred during the fifth reproductive period (Fig. 2). Although reproductive condition of males was not implicated as the cause of cessation of breeding in previous studies of Nuttall's cottontails (Powers and Verts, 1971; McKay and Verts, 1978a), Brambell (1944) reported that cessation of breeding among European rabbits was related to decreased fecundity of males.

Maintenance of higher levels of activity among adult females than among adult males after the reproductive season may be related to the production and care of the last litter, and to subsequent needs for physiological recovery from production of four or five successive litters. In a study of foraging behavior of hoary marmots (Marmota caligata), Barash (1980) found that postreproductive females spent a greater percentage of their time foraging than marmots in other segments of the population.

Observations of juvenile Nuttall's cottontails suggested that low-level, secretive activity during daytime within the first 1 to 2 months of life may be an adaptive strategy employed by cottontails to reduce risks of predation. Lechleitner (1958) noted that young black-tailed jackrabbits were extremely wild and rarely seen. Similarly, Vorhies and Taylor (1933) reported that juvenile jackrabbits (L. californicus and L. alleni) were wilder, more nocturnal, and less likely to leave cover than adults. Juvenile jackrabbits raised by Lechleitner (1958) were active only at night until they were about 2 months old, then a gradual shift to more diurnal activity began.

Considerable variation exists among published accounts of diel activity patterns of lagomorphs. Several investigators tried to relate activity levels to sunrise and sunset, but no definitive pattern emerged from their work. Lord (1964) reported that penned cottontails were moderately active all day, and that onset of activity was not sudden. He observed a bimodal pattern of activity, with evening and early morning peaks, but suggested that sunset and sunrise were not the main stimuli for onset and termination of activity. Observations of cottontails in a 0.8-ha enclosure by Holler and Marsden (1970) produced results similar to those reported by Lord (1964). In contrast, Mech et al. (1966) reported relationships between onset of activity and sunset, cessation of activity and sunrise, and duration of activity and duration of darkness for eastern cottontails and snowshoe hares; however, they admitted that variation

within and among individuals indicated the influence of factors other than sunset and sunrise on activity patterns.

Daily activity patterns in lagomorphs commonly were reported to be influenced by season, extremes in temperature, moisture, and habitat. For example, Ingles (1941) reported that for desert cottontails (Sylvilagus audubonii) minimum activity occurred between 0900 and 1500 h and greatest activity occurred between sunset and 0900 h; however, cottontails were active every hour of day and night, and time of greatest activity differed from month to month. Vorhies and Taylor (1933) observed similar changes in daily activity of jackrabbits. Also, Lee et al. (1941) reported that the maximum air temperature that domestic rabbits could tolerate continuously was about 33 to 35° C, and Johnson et al. (1958) found, that above 20° C, respiration rates of domestic rabbits increased at a gradual, uniform rate from approximately 90 respirations/min to nearly 200/min at 40° C. Based on relationships discussed by Schmidt-Nielson (1979), a 1 kg rabbit that remained on a hot desert floor during an average day, and utilized physiological mechanisms to dissipate heat by evaporation, would use approximately 7.5% of its body mass in water/h. Barnett (in litt.) suggested that heat loss from eastern cottontails at 0° C was substantial, and that penned cottontails were more observable when air temperature increased above 5° C. In the laboratory, he demonstrated behavioral selection by cottontails of a chamber insulated with artificial infrared radiation at 0° C, no selection at 15° C, and selection of a noninsulated chamber at 35° C.

Available moisture, in the form of green vegetation, seemingly was related to onset of breeding and to maintenance of relatively high levels of productivity among leporids (Ingles, 1941; Fitch, 1947; Mossman, 1955; Hunt, 1959). For Nuttall's cottontails in central Oregon, McKay and Verts (1978a) suggested that onset of drought periods possibly were responsible for cessation of breeding, and Hundertmark (1982) demonstrated a relationship between juvenile survival and precipitation.

The observed pattern of daily activity among Nuttall's cottontails seemed to reflect temperature and moisture constraints. The early morning peak of activity coincided with increasing ambient temperature and near-maximum availability of water in plants. At night in the desert, decrease in temperature causes an increase in relative humidity of air, and dry plant material absorbs moisture; African grasses and shrubs favored by oryx (Oryx gazella) contained as little as 1% water during the day, but increased to 42% water after 10 h of exposure to air that simulated a desert night (Taylor, 1969). After the morning peak, cottontail activity declined gradually as air temperatures rose and plant moisture content decreased. The midday lull in activity corresponded with maximum air temperatures and minimum plant water content, and a smaller peak of activity after sunset coincided with reduction of air temperatures to more favorable levels. Evening was not a period of optimal plant moisture, but metabolic demands may have necessitated activity (feeding) anyway.

Examination of various components of the activity budget of Nuttall's cottontails suggested that cottontail behavior (type,

timing, frequency, and duration of), like activity patterns, was related to environmental constraints, and was directed toward maintenance of a favorable energy balance. Acquisition of food, and of water within that food, obviously was a critical activity for cottontails, as indicated by the high percentage of time they spent feeding. Timing of feeding activity and selection of food items by cottontails seemed to be directed toward optimizing moisture gain from plant materials. My observations of extensive use of grasses during spring and early summer, and selection of juniper as a food item in late summer were consistent with Hundertmarks' (1982) findings from a more detailed study of food habits of Nuttall's cottontails, based on analyses of stomach contents. After examining seasonal relationships among distribution of precipitation, forage abundance, plant succulence, and food habits of cottontails, Hundertmark (1982) concluded that cottontails selected the most succulent and nutritious foods of those available.

Tree-climbing may be an adaptation for acquiring water in times of moisture stress (Verts et al., in press). Relatively low nutritive value (Dietz et al., 1962; Smith, 1952, 1957; Vaughan, 1982), presence of relatively large amounts of terpenoid compounds (Schwartz et al., 1980a, b), and seasonal foraging on juniper suggested that consumption of juniper was not solely for the purpose of meeting energy requirements. On numerous occasions during July and August 1981, juniper foliage was covered with droplets of water during early morning hours. Plastic bags tightly secured around juniper boughs

collected water overnight, indicating that water exuded from within the trees. Thus, tree-climbing provided cottontails access to available water, in the form of droplets on juniper foliage or waterlogged foilage. Most tree-climbing occurred during the first hour after sunrise, and corresponded to a time of near-maximum water content in desert plants (Taylor, 1969).

Timing of resting bouts, along with position and posture of resting cottontails, suggested that resting was related to thermoregulation. In early morning, cottontails frequently sat motionless in a hunched posture in relatively open areas near cover, seemingly waiting for the morning sun to warm them. Barnett (1977) showed that below thermoneutrality an increase in radiant energy lowered the critical ambient temperature at which eastern cottontails had to increase their metabolic rates to maintain body temperature; thus, basking during cold days considerably reduced thermoregulatory costs for cottontails. Time spent resting increased considerably during the fourth hour after sunrise and remained relatively high throughout midday hours. The high proportion of time spent resting under cover or in rock crevices during warm hours of late morning and afternoon may, in part, be responsible for low frequency of observation of cottontails during these periods. During evening periods cottontails rested in shade of trees or shrubs until the sun began to set and the ambient temperature began to decline. These observations corroborated Barnett's (1977) finding that cottontails selected conditions that favored thermoneutrality and minimal energy expenditure.



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## APPENDIX

Table A. Pearson's correlation coefficients for combinations of Nuttall's cottontail activity indices and environmental variables, for data collected on the Terrebonne study area, Deschutes County, Oregon, during 1981 observation periods, 1981 and 1980 trapline cruises, 1981 Area A cruises, and 1981 and 1980 trapping periods.<sup>a</sup>

	DATE	REPROPER	DAY REPRO	CTIME	RTIME	OWLS	TIMEOWL P	TIMEOWL A	HAWKS	AVIAN
OBSERVATION PERIODS (Number observed/h)										
Total	0.04	0.01	0.06	-0.09	-0.08	0.11	0.05	-0.11	-0.07	0.05
Adult Male	-0.34*	-0.32*	-0.28*	-0.08	-0.06	0.29*	0.29*	-0.05	0.01	0.23*
Adult Female	0.04	0.12	-0.05	-0.16*	-0.16	0.01	0.02	-0.04	-0.04	-0.01
Adult	-0.21*	-0.13	-0.22*	0.08	0.07	0.21*	0.18*	-0.05	-0.03	0.14*
Juvenile Male	0.67*	u	0.67*	0.08	0.09	-0.03	-0.14	-0.15	-0.14	-0.07
Juvenile	0.61*	u	0.61*	0.02	0.01	-0.04	-0.19*	-0.18*	0.08	-0.01
(Time in view/h)										
Total	0.38*	0.26*	0.40*	-0.10	-0.10	-0.17	-0.17	-0.14	-0.20*	-0.23*
Adult Male	-0.24*	-0.23*	-0.19*	-0.14*	-0.11	0.23*	0.22	-0.05	-0.03	0.16*
Adult Female	0.09	0.16*	-0.01	-0.16*	-0.16*	-0.08	-0.07	-0.05	-0.16*	-0.15*
Adult	0.01	0.08	-0.06	-0.12	-0.12	-0.01	0.01	-0.05	-0.17*	-0.09
Juvenile Male	0.60*	u	0.60*	0.08	0.10	-0.08	-0.11	-0.13	-0.12	-0.12
Juvenile	0.59*	u	0.59*	0.07	0.07	-0.10	-0.13	-0.15	0.02	-0.10
1981 TRAPLINE CRUISES (Number observed/h)										
Total	0.40*	0.25*	0.42*	-0.14*	-0.29*	0.21*	-	-	-0.15	0.09
Adult Male	-0.31*	-0.41*	-0.20*	0.07	0.06	0.14	-	-	0.21*	0.22*
Adult Female	-0.08	-0.08	-0.06	-0.10	-0.09	0.21*	-	-	-0.03	0.15
Adult	-0.07	-0.17	<-0.01	-0.09	-0.08	0.20*	-	-	-0.03	0.15
Juvenile Male	0.43*	0.26*	0.47*	-0.11	-0.25*	0.20*	-	-	-0.08	0.12
Juvenile Female	0.52*	0.29*	0.57*	0.02	-0.19*	0.06	-	-	-0.14	-0.02
Juvenile	0.54*	0.45*	0.50*	-0.10	-0.30*	0.11	-	-	-0.15	0.01
1981 AREA A CRUISES (Number observed/h)										
Total	0.20*	0.31*	<0.01	-0.20*	0.01	0.11	-	-	0.05	0.11
Adult Male	-0.43*	-0.37*	-0.39*	0.03	0.27*	<0.01	-	-	0.30*	0.07
Adult Female	0.20*	0.33*	-0.02	-0.23*	-0.07	0.07	-	-	0.01	0.06
Adult	-0.09	0.04	-0.22*	-0.21*	-0.08	0.02	-	-	0.12	0.05
Juvenile Male	0.64*	0.39*	0.77*	-0.26*	-0.19*	0.12	-	-	0.08	0.09
Juvenile Female	u	u	u	u	u	u	-	-	u	u
Juvenile	0.55*	0.55*	0.39*	-0.24*	-0.16	0.21*	-	-	-0.10	0.16
1980 TRAPLINE CRUISES (Number observed/h)										
Total	0.13	-	-	-	-0.15	0.31*	-	-	0.07	0.30*
Adult	u	-	-	-	u	u	-	-	u	u
Juvenile	0.12	-	-	-	-0.07	0.21	-	-	0.01	0.18
1981 TRAP DATA (Number of captures/night)										
Total	-0.67*	-0.48*	-0.68*	-	-	-	-	-	-	-
Adult Male	-0.69*	-0.72*	-0.57*	-	-	-	-	-	-	-
Adult Female	-0.57*	-0.47*	-0.54*	-	-	-	-	-	-	-
Adult	-0.81*	-0.78*	-0.70*	-	-	-	-	-	-	-
Juvenile Male	-0.05	0.14	-0.14	-	-	-	-	-	-	-
Juvenile Female	-0.16	0.11	-0.30*	-	-	-	-	-	-	-
Juvenile	-0.13	0.16	-0.27*	-	-	-	-	-	-	-
1980 TRAP DATA (Number of captures/night)										
Total	-0.14	-	-	-	-	-	-	-	-	-
Adult Male	-0.09	-	-	-	-	-	-	-	-	-
Adult Female	-0.48*	-	-	-	-	-	-	-	-	-
Adult	-0.40*	-	-	-	-	-	-	-	-	-
Juvenile Male	0.20	-	-	-	-	-	-	-	-	-
Juvenile Female	<0.01	-	-	-	-	-	-	-	-	-
Juvenile	0.13	-	-	-	-	-	-	-	-	-

<sup>a</sup> definitions of symbols and acronyms for variables appear on page following table.

Table A. Continued

	MINTEMP	MAXTEMP	MEANT	MINTEMP2	MAXTEMP2	PRECIP3	PRECIP4	MINCC	MAXCC	MEANCC
OBSERVATION PERIODS (Number observed/h)										
Total	-0.21*	-0.19*	-0.21*	-0.13	0.06	<0.01	0.09	-0.16*	-0.08	-0.12
Adult Male	-0.25*	-0.32*	-0.29*	-0.34*	-0.32*	0.10	-0.23*	0.05	0.17*	0.12
Adult Female	-0.19*	-0.20*	-0.20*	-0.06	-0.03	-0.03	-0.05	-0.09	-0.08	-0.09
Adult	-0.31*	-0.32*	-0.33*	-0.30*	-0.25*	0.06	-0.18*	-0.05	0.03	-0.01
Juvenile Male	0.11	0.24*	0.18*	0.38*	0.43*	-0.26*	0.06*	-0.23*	-0.13	-0.18*
Juvenile	0.01	0.012	0.07	0.25*	0.34*	-0.12	0.57*	-0.26*	-0.18	-0.22*
(Time in view/h)										
Total	0.03	0.06	0.04	0.26*	0.33*	-0.05	0.39*	-0.27*	-0.28*	-0.29*
Adult Male	-0.18*	-0.29*	-0.25*	-0.20*	-0.24*	0.09	-0.16*	0.08	0.21*	0.16*
Adult Female	-0.09	-0.12	-0.11	0.09	0.14*	0.05	-0.04	-0.17*	-0.20*	-0.20*
Adult	-0.14*	-0.19*	-0.17*	<0.01	0.05	0.06	-0.08	-0.13	-0.13	-0.14*
Juvenile Male	0.08	0.22*	0.16	0.32*	0.35*	-0.22*	0.63*	-0.21*	-0.17	-0.19*
Juvenile	0.03	0.17	0.11	0.26*	0.31*	-0.15	0.60*	-0.22*	-0.18	-0.20*
1981 TRAPLINE CRUISES (Number observed/h)										
Total	0.12	0.27*	0.21*	0.36*	0.38*	-0.24*	0.42*	-0.21*	-0.21*	-0.21*
Adult Male	-0.31*	-0.32*	-0.33*	-0.21*	-0.27*	-0.13	-0.13	0.20*	0.07	0.14
Adult Female	-0.11	-0.07	-0.09	-0.04	-0.01	-0.23*	<-0.01	0.05	0.08	0.07
Adult	-0.22*	-0.12	-0.17	-0.04	-0.02	-0.17	-0.03	0.02	-0.04	-0.01
Juvenile Male	0.18*	0.26*	0.23*	0.30*	0.34*	-0.14	0.45*	-0.29*	-0.27*	-0.29*
Juvenile Female	0.36*	0.40*	0.40*	0.47*	0.47*	-0.16	0.59*	-0.29*	-0.23*	-0.26*
Juvenile	0.33*	0.42*	0.40*	0.48*	0.51*	-0.17	0.52*	-0.28*	-0.24*	-0.27*
1981 AREA A CRUISES (Number observed/h)										
Total	0.11	0.18	0.15	0.16	0.22*	0.15	0.03	-0.14	-0.09	-0.12
Adult Male	-0.24	-0.26*	-0.26*	-0.35*	-0.36*	0.11	-0.28*	0.29*	0.29*	0.29
Adult Female	0.19*	0.21*	0.20*	0.18	0.24*	<0.01	0.02	-0.21*	-0.16	-0.19
Adult	<-0.01	<0.01	<-0.01	-0.06	-0.02	0.15	-0.16	-0.03	0.02	-0.01
Juvenile Male	0.18	0.35*	0.27*	0.56*	0.64*	-0.31*	0.62*	-0.33*	-0.32*	-0.32*
Juvenile Female	u	u	u	u	u	u	u	u	u	u
Juvenile	0.21*	0.34*	0.28*	0.41*	0.50*	0.01	0.23*	-0.26*	-0.25*	-0.26*
1980 TRAPLINE CRUISES (Number observed/h)										
Total	0.13	0.24	-	-	-	-0.07	0.06	-	-	-
Adult	u	u	-	-	-	u	u	-	-	-
Juvenile	0.25	0.45	-	-	-	-0.25*	0.08	-	-	-
1981 TRAP DATA (Number of captures/night)										
Total	-	-	-	-0.65*	-0.68*	0.33*	-0.62*	-	-	-
Adult Male	-	-	-	-0.60*	-0.66*	0.29*	-0.46*	-	-	-
Adult Female	-	-	-	-0.47*	-0.55*	0.29*	-0.48*	-	-	-
Adult	-	-	-	-0.69*	-0.78*	0.36*	-0.59*	-	-	-
Juvenile Male	-	-	-	-0.11	-0.05	-0.03	-0.13	-	-	-
Juvenile Female	-	-	-	-0.27*	-0.25*	0.21*	-0.37*	-	-	-
Juvenile	-	-	-	-0.23*	-0.18	0.11	-0.31*	-	-	-
1980 TRAP DATA (Number of captures/night)										
Total	-	-	-	-0.26*	-0.42*	0.14	-0.06	-	-	-
Adult Male	-	-	-	-0.12	-0.24	0.08	-0.05	-	-	-
Adult Female	-	-	-	-0.16	-0.34*	0.10	-0.35*	-	-	-
Adult	-	-	-	-0.18	-0.38*	0.11	-0.28*	-	-	-
Juvenile Male	-	-	-	0.06	<0.01	-0.17	0.21	-	-	-
Juvenile Female	-	-	-	-0.34*	-0.35*	0.27*	0.01	-	-	-
Juvenile	-	-	-	-0.21	-0.26*	0.10	0.14	-	-	-

u definitions of symbols and acronyms for variables appear on page following table.

Table A. Continued

	WINDMIN	WINDMAX	MEANW	NIGHT	TIMEILL	FRACILL	BEGINILL	ENDILL	MPHASE	ILLUM
OBSERVATION PERIODS (Number observed/h)										
Total	-0.21*	-0.16*	-0.18*	0.03	0.06	-0.02	0.14*	<-0.01	-0.14*	-0.04
Adult Male	-0.09	-0.06	-0.07	0.21*	0.16*	0.01	0.22*	-0.08	-0.17*	0.05
Adult Female	-0.21*	-0.18*	-0.20*	-0.15*	-0.06	-0.04	0.01	0.01	-0.10	-0.08
Adult	-0.17*	-0.14*	-0.16*	0.04	0.07	-0.04	0.14*	-0.03	-0.18*	-0.03
Juvenile Male	-0.09	0.07	0.04	0.69*	0.29*	0.18*	0.17	0.14	-0.03	0.24*
Juvenile	-0.12	0.01	-0.02	0.61*	0.27*	0.18*	0.17	0.09	-0.01	0.21*
(Time in view/h)										
Total	-0.19*	-0.17*	-0.18*	-0.07	-0.04	0.03	-0.02	0.01	0.07	-0.06
Adult Male	-0.09	-0.09	-0.10	0.13	0.10	0.03	0.17*	-0.04	-0.08	0.05
Adult Female	-0.17*	-0.18*	-0.19*	-0.19*	-0.05	0.07	-0.07	-0.03	0.03	-0.02
Adult	-0.19*	-0.19*	-0.20*	-0.13	-0.01	0.06	-0.01	-0.05	<-0.01	-0.01
Juvenile Male	-0.03	0.07	0.05	0.65*	0.18*	0.06	0.08	0.10	0.05	0.07
Juvenile	-0.04	0.05	0.03	0.63*	0.18	0.06	0.11	0.08	0.03	0.06
1981 TRAPLINE CRUISES (Number observed/h)										
Total	0.05	-0.18	-0.14	0.15	0.19*	0.16	0.21*	-0.10	<0.01	0.18
Adult Male	0.30*	0.16	0.20	0.30 *	0.02	-0.14	0.18	0.23*	-0.20*	-0.09
Adult Female	0.08	-0.05	-0.02	0.08	0.02	<-0.01	0.08	-0.05	0.03	-0.04
Adult	0.10	-0.13	-0.08	0.14	0.15	0.07	0.24*	-0.10	-0.14	0.06
Juvenile Male	-0.08	-0.13	-0.13	0.18	0.14	0.16	0.15	-0.04	0.04	0.19*
Juvenile Female	-0.01	-0.13	-0.11	0.26*	0.28*	0.25*	0.05	-0.05	0.22*	0.27*
Juvenile	-0.04	-0.13	-0.12	0.05	0.12	0.15	0.11	-0.03	0.11	0.07
1981 AREA A CRUISES (Number observed/h)										
Total	-0.12	0.02	-0.02	-0.34*	-0.11	-0.04	-0.03	-0.23*	-0.04	-0.10
Adult Male	0.03	0.19*	0.15	0.27*	0.22*	0.03	0.07	-0.18*	-0.10	0.11
Adult Female	-0.12	-0.01	-0.04	-0.35*	-0.22*	-0.09	-0.26	-0.16	0.20*	-0.18*
Adult	-0.07	0.09	0.05	-0.11	<-0.01	-0.02	-0.10	-0.23*	0.04	-0.03
Juvenile Male	-0.07	-0.08	-0.08	-0.15	0.10	0.30*	0.28*	0.07	<0.01	0.19*
Juvenile Female	u	u	u	u	u	u	u	u	u	u
Juvenile	-0.15	-0.15	-0.16	-0.48*	-0.20*	-0.02	0.08	-0.13	-0.11	-0.12
1980 TRAPLINE CRUISES (Number observed/h)										
Total	-	-	-	0.05	-0.14	-0.16	0.06	0.15	-0.16	-0.18
Adult	-	-	-	u	u	u	u	u	u	u
Juvenile	-	-	-	0.02	-0.23*	-0.21	-0.06	0.07	-0.16	-0.24*
1981 TRAP DATA (Number of captures/night)										
Total	-	-	-	-0.17	-0.08	-0.18	-0.01	0.05	-0.20*	-
Adult Male	-	-	-	0.32*	0.16	-0.06	0.14	0.05	-0.20	-
Adult Female	-	-	-	-0.06	-0.06	-0.13	0.10	0.13	-0.27*	-
Adult	-	-	-	0.22*	0.09	-0.11	0.16	0.10	-0.28*	-
Juvenile Male	-	-	-	-0.39*	-0.15	-0.10	-0.16	-0.03	0.07	-
Juvenile Female	-	-	-	-0.47*	-0.23*	-0.17	-0.18	-0.04	-0.06	-
Juvenile	-	-	-	-0.53*	-0.24*	-0.16	-0.21*	-0.04	0.01	-
1980 TRAP DATA (Number of captures/night)										
Total	-	-	-	-0.04	0.07	0.07	-0.04	-0.14	0.03	-
Adult Male	-	-	-	-0.05	-0.17	-0.16	-0.13	0.02	0.05	-
Adult Female	-	-	-	-0.33*	-0.04	-0.08	0.15	0.15	-0.16	-
Adult	-	-	-	-0.27*	-0.12	-0.13	0.05	0.13	-0.10	-
Juvenile Male	-	-	-	0.21	0.01	0.04	-0.04	-0.20	-0.09	-
Juvenile Female	-	-	-	0.03	0.26*	0.25*	-0.07	-0.21	0.22	-
Juvenile	-	-	-	0.16	0.21	0.22	-0.07	-0.28*	0.10	-

<sup>a</sup> definitions of symbols and acronyms for variables appear on page following table.

a \* denotes values significant at  $P \leq 0.05$ .

u denotes values that could not be calculated.

- denotes variables not included in particular data sets.

Descriptions of environmental variables: DATE (day of year), REPROPER (reproductive period), DAYREPRO (day of 26-day reproductive period), CTIME (clock time), RTIME (time relative to sunrise or sunset), OWLS (number of owls observed per hour), TIMEOWLP (time owls present), TIMEOWLA (time owls active), HAWKS (number of hawks observed per hour), AVIAN (total number of avian predators observed per hour), MINTEMP, MAXTEMP, MEANT (minimum, maximum, and mean ambient temperatures during the period), MINTEMP2, MAXTEMP2 (minimum and maximum temperatures for the previous day), PRECIP3 (number of consecutive days with precipitation), PRECIP4 (number of consecutive days without precipitation), MINCC, MAXCC, MEANCC (minimum, maximum, and mean cloud cover during the period), WINDMIN, WINDMAX, MEANW (minimum, maximum, and mean wind speed during the period), NIGHT (length of the previous night [or current night, for nighttime observation periods and for trapping data]), TIMEILL (duration of lunar illumination during the night), FRACILL (fraction of moon illuminated), BEGINILL, ENDILL (time lunar illumination began and ended), MPHASE (phase of moon), ILLUM (index to lunar illumination =  $\text{TIMEILL} \times \text{FRACILL}$ ).