Population Limitation of Jackrabbits: an Examination of the Food Hypothesis

William R. Clark
Utah State University

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POPULATION LIMITATION OF JACKRABBITS: AN EXAMINATION OF THE FOOD HYPOTHESIS

by

William R. Clark

A dissertation submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Wildlife Ecology

Utah State University
Logan, Utah

1979
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William R. Clark

William R. Clark
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ABSTRACT

Population Limitation of Jackrabbits: An Examination of the Food Hypothesis

by

William R. Clark, Doctor of Philosophy

Utah State University, 1979

Major Professor: Dr. George S. Innis
Department: Wildlife Science

The study was conducted to examine the importance of forage resources in limiting peak population density of black-tailed jackrabbits (Lepus californicus). The research design combined field studies of jackrabbit diet and vegetation impact with computer simulation of herbivore nutrition and population dynamics. The relationships between available forage, dietary intake, energy and protein balance and population changes were compared for high and low population density. Hypotheses tested were: (1) Dietary composition is unaffected by availability above 10 kg/ha; (2) Jackrabbits do not require more forage than is available at high population densities; (3) Dietary composition is not significantly different at high and low densities; (4) Dietary composition is not significantly different between sexes; (5) Nutritional balance of lactating females is not significantly altered at high density; and (6) Nutritional balance of females entering the breeding season is not significantly altered at high density.
The field studies were designed to measure dietary preference by the jackrabbits, the availability of herbage, and utilization of selected plant species. Jackrabbits ate nearly all forage types available but primarily consumed dominant shrubs in fall and winter, suffrutescents in fall and winter, grasses in spring and summer, and forbs in summer. There was no significant difference between dietary composition or preference rating among density periods or sexes. Dietary percentage of preferred forage species was directly related to availability above 10 kg/ha. Jackrabbits removed an average of 30 to 40 percent of individual plants of *Kochia americana*, but only browsed on 5 to 11 percent of all available plants. Total removal of *Kochia* standing crop averaged only 3.7 percent.

The model used in the simulation studies incorporated relationships involving existence, activity and production (growth, gestation and lactation) requirements to estimate forage requirements. Intake and requirements affect energy and protein balance which are related to body weight changes and production. Model mortality rates are modified by nutritional deficiency as a fraction of the requirements.

The following conclusions resulted from model simulations. Forage requirements are less than 1 percent of available forage, even at high population density. Nutritional balance of lactating females was unaffected by observed diets or population density. Nutritional balance of females entering the breeding season is unaffected by diet but may be affected by early breeding date or large litter size. Individual nutritional response and its interaction with food does not cause significant change in population mortality.
rates. Nutritional deficiency may contribute to mortality, particularly during lactation or winter periods, but these effects are independent of population density.
INTRODUCTION

Population Regulation

The factors that determine the dynamics of populations of vertebrates have received substantial attention in literature of population ecology. Many hypotheses on regulatory mechanisms have emerged, including both environmental and intrinsic relationships (Lidicker 1978). In many cases the hypotheses investigated have been determined in part by the species and the circumstances. Insect ecologists have been impressed by density-independent factors such as weather; rodent ecologists by density-dependent factors such as physiological stress, genetic changes, predation and dispersal; avian ecologists by food shortage and behavioral mechanisms; and large mammal ecologists by predation, disease, and food shortage. The result has been competition among many hypotheses that purport to explain what regulates (keeps population numbers within some upper and lower bounds) population numbers.

Andrewartha and Birch (1954) expressed the view that populations were prevented from indefinite increases by factors independent of density, such as changes in weather patterns. Food availability, they believed, was not related to density but to the onset of poor weather conditions.

Lack (1954) suggested that food resources were limiting to vertebrates in general, especially birds. Direct food limitation in mammals he considered less widespread but certainly important. He
believed that the food supply hypothesis of regulation had not been considered carefully enough at high densities of herbivores.

Hairston et al. (1960) argued that the herbivore trophic level as a whole could not be limited by food resources and must be directly limited by predators. The eruption of deer on the Kaibab plateau after reduction of their predators, is often cited in support of the predation hypothesis. Mech (1975) and Hirst (1969) have presented convincing evidence that large predators are preventing populations of ungulates from increasing. Pearson (1966) and Gibb (1977) have suggested similar ideas for populations of rodents and lagomorphs, respectively.

The idea that declines in populations could be associated with changes in adrenal-pituitary functions was proposed by Christian (1950). The general hypothesis (Christian 1961) is that mammals limit their own densities by behavioral and physiological changes. The specific thesis is that the mechanism of this limitation is associated with physiological stress and the changes are purely phenotypic.

In contrast, Chitty (1960) and Krebs and Myers (1974) postulated that density-dependent genetic selective pressure reduce viability through changes in behavior and physiology. A key difference between these ideas and those of Christian is that the population density lags somewhat behind the changing selective pressures so that no stable equilibrium occurs. This hypothesis has been proposed to explain population oscillations in microtine rodents.

Wynne-Edwards (1965) hypothesized that animals rarely if ever reach the maximum density allowed by their food resources and thus
must be self-regulated below that level. Communal displays to "sense" density intermittently occur and feedback to population demographic variables causes a change in population density.

Behavioral regulation of population density of a different sort seems to operate for some populations. Dominance, spacing behavior, aggression, and dispersal play an important part in regulating the populations of red grouse (Lagopus l. scoticus) and Uinta ground squirrels (Spermophilus armatus) according to Watson and Moss (1970) and Salde and Balph (1974) respectively. The implication is that these populations are regulated below the level at which food resources become limiting.

In many cases the above hypothesized mechanisms undoubtedly interact to produce the dynamics of a population. Specific population demographic changes may be explained by one or another hypothesis. In some studies, notably long-term studies, more complex patterns composed of these hypothesized mechanisms have been proposed to explain the annual fluctuations in numbers of animals. One conceptual model of showshoe hare (Lepus americanus) population fluctuations involves the food limitation and predation hypotheses (Keith 1974, Keith and Windberg 1978). Studies of Scottish red grouse have led to a hypothesis including components of behavior, food limitations with nutritional consequences, and genetics (Watson and Moss 1972). Population studies (Ehrlich et al. 1975) of checkerspot butterflies (Euphydryas spp.) have emphasized that such hypotheses may be dependent on local conditions, and may actually be contradictory for a species under different circumstances.
Food Resource Interactions

Most of the above hypotheses imply that population changes occur before food resources are depleted. There are, however, a number of ideas in the literature that include direct involvement of food resources. Observations that plants are seldom defoliated and vegetation is abundant are dangerous reasons for discounting plant-herbivore relations in ecosystems (Harper 1969). Chew (1974) has offered some alternatives to total consumption as possible mechanisms whereby plant populations may be affected by and affect herbivores. Physical activities, selectivity in feeding and timing of consumption can influence plant-herbivore responses. Murdoch (1966) has said that it is dangerous to use observations that animals do not starve to death, except in extreme conditions, to reject the food hypothesis.

Plant-herbivore systems are highly co-evolved systems, and feedback mechanisms are central to the effect of food resources on herbivore dynamics. Selective grazing by herbivores has been reported to decrease plant diversity and production (Harper 1969, Chew 1974) and these changes may affect the numbers of herbivores. Myers and Poole (1963) have shown exactly this kind of feedback in rabbit (Oryctolagus cuniculus) populations in Australia. If there is a delay in the feedback, the nature of feedback systems is disrupted and oscillations may occur (Forrester 1961, May 1973). Variables such as the plant species, vigor of the plants, season and intensity of use, and extent of defoliation may affect the rate of recovery of the system (Cook 1971).
The relationship between plants and animals is further complicated by selective feeding. Most animals exhibit preferences, and these are not always for the most abundant foods (Gardarsson and Moss 1970, Westoby 1974, see Pyke et al. 1977 for review). Nutrient content can be important to palatability, digestibility and selectivity, however, there is no consistent relationship between these characteristics of forage and its nutrient content (Arnold 1964, Hughes et al. 1964). Succulence, color, smell, and taste may be proximal stimuli used by herbivores to select forage. Herbivores may select their diet on the basis of a single characteristic (for example, water content) and neglect other characteristics of the plants. Behavioral characteristics of the animals in response to differences in vegetation and other stimuli (predators, reproductive functions) prevent animals from using all of the available forage (Arnold 1964). Seasonal changes in the forage quality influence the animals' selectivity and change their impact on the vegetation (Cook and Harris 1968, Miller 1968, Feeny 1970).

Population fluctuations in some vertebrates are related to periodic food depletions. Thompson (1955) and Pitelka (1957) held this view about the lemming cycles in the Arctic. In peak years, lemmings depress production of food and cover by 99 percent. Krebs (1964) rejected this view of lemming cycles because no evidence of nutritional deficiencies was found in the lemmings.

Frequently, food shortage is associated with decreases in body weights and increases in mortality. Murton et al. (1966) found that the proportion of wood pigeons in low weight classes varied in
relation to the mortality rates and population weight variation was correlated with the clover food supply. Keith (1974) and Keith and Windberg (1978) postulated that snowshoe hares at high densities deplete their overwinter browse supply. Food shortage results and hares cannot maintain their body weights. Juvenile, and eventually adult, mortality increases, thus initiating a population decline.

The forage available in desert climates often influences mammalian breeding. Reichmann and Van de Graff (1975) and Pinter and Negus (1965) showed that reproduction in desert rodents is triggered by increased availability of green forage. Newsome (1966) postulated that breeding of kangaroos depends mainly on the abundance of food, especially after droughts break.

The quality of food resources has been offered as another explanation of population limitation in vertebrates. Nutrient content of the forage is frequently related to secondary production (Cook and Harris 1968). Freeland (1964) postulated that vole cycles may be related to depletion of non-toxic preferred foods and increases in toxic foods in the diet. Phytoestrogens have been related to mammalian reproduction (Labov 1977). The quality of heather (Calluna vulgaris) was directly related to the breeding success and subsequent population density of red grouse (Miller et al. 1970).

Nutritional effects can carry over to subsequent generations. In red grouse, Watson and Moss (1971) found that population changes were related to chick survival, which was related to nutrition of adults. Furthermore, poor nutrition depresses breeding success and causes the young to select larger territories the following year.
The nutritional effect is delayed by 1 year and essentially regulates the population density. Cowley and Griesel (1966) showed similar carryover effects of nutrition on the growth and reproduction of rats fed low protein diets.

Large ungulates are often viewed as being food limited, especially by the availability of high quality forage. Klein (1970), in reviewing research on North American deer populations, found that early post-natal mortality of fawns from does suffering poor nutrition can be a limiting factor in deer populations. Taber and Dasmann (1957) found that mortality among California black-tailed deer (Odocoileus hemionus columbianus) was seasonal in character, a result of changes in forage nutrient content, but not quantitative drop in available forage. Sinclair (1974) showed that the food supply regulates African buffalo (Syncerus caffer) populations in a density-dependent way. Crude protein of the forage drops below maintenance levels during the dry season for some of these populations. In others, the available quantity of forage drops below the population requirements. Mortality of adults caused by malnutrition acts as a regulating factor in all cases.

It can be seen from this review that under certain conditions, food resources may act as a limiting factor on herbivore populations. For this study the mechanisms which constitute the food hypothesis are as follows. When availability of forage is low, the actual rate of increase of the population may be reduced to zero or be made negative. The interactions of the population with its forage resources must be mediated through the nutritional/physiological systems of
the individuals in the population (Heasley 1977). The limitation may be quantitative; that is, there is insufficient forage energy available to sustain larger numbers of individuals. It may be qualitative; that is, there may be a shortage of the proper quality forage (e.g., protein, macro- or micro-nutrients).
OBJECTIVES AND APPROACH

The objective of this study was to examine the role that forage plays in limiting peak populations of one herbivore, the black-tailed jackrabbit (Lepus californicus). Studies of black-tailed jackrabbits have considered other aspects of their ecology in relation to population dynamics, particularly the role of predation. Mechanisms by which forage limitations affect this herbivore's population dynamics are stated for a specific system. While the general implications of resource limitation on herbivore population are open to interpretation, other consequences of forage limitation are testable.

The Rangeland-Jackrabbit-Livestock-Coyote System

The rangeland-jackrabbit-livestock-coyote system of the Great Basin desert is a system with similar characteristics to those plant-herbivore systems for which resource limitation has been suggested. Black-tailed jackrabbit populations are known to fluctuate widely over much of the species' range. As a result of long-term demographic studies in Curlew Valley, northern Utah, Gross et al. (1974) concluded that these changes are of an oscillatory form. Density of jackrabbits in Curlew Valley has changed from 12 rabbits/km² to 102 rabbits/km², from low to peak density populations (Stoddart 1975).

During population increases, overwinter total population survival is much higher than during declines. Spring to fall survival
of both adults and juveniles is higher during increases than during declines. During peak and declining populations juvenile survival decreases first and then adult survival also decreases. These variations in survival are largely responsible for the observed density changes. Natality does vary, but has little effect on the population fluctuations (Gross et al. 1974, Stoddart 1977).

Wagner and Stoddart (1972) showed that coyote (Canis latrans) predation influences the oscillations in large part. However, because jackrabbits increase faster than coyotes, they may be essentially released from coyote predation as the major source of mortality at high densities. "Other mortality sources--disease, exhaustion of the food supply or pituitary-adrenal stress, or both--will presumably be needed to reverse the population trend, induce the decline, and enable the now-abundant coyotes once again to assume dominance over the prey" (Wagner and Stoddart 1972:341).

Stoddart (1975) used k-factor analysis (see Varley et al. 1973) to identify some of the mortality factors associated with density changes. He concluded that factors other than coyote predation were responsible for a large part of the adult jackrabbit spring to fall mortality. Furthermore, during the period of peak densities, mortality among juveniles from coyotes was replaced by mortality from an unidentified, density related factor and then by some unknown "carry-over" effect. Food shortage among vertebrates, as outlined in the food limitation hypothesis of this study, is consistent with these patterns. Under the hypothesis, food shortage causes mortality
associated with the density related factors or the "carry-over" effects identified by Stoddart (1975).

The jackrabbit competes with livestock for forage (Vorhies and Taylor 1933, Currie and Goodwin 1966) on winter ranges of the Great Basin. Apparently there were significant changes in the Great Basin desert in the early part of this century in both the quantity and composition of the forage vegetation as a result of sheep and cattle grazing (Kearney et al. 1914, Holmgren and Hutchings 1971). Ellison (1960) concluded that jackrabbits increase on overgrazed ranges due to increased proportions of forbs and shrubs. Such changes serve to enhance the jackrabbit-vegetation interactions by changing herbivore selectivity and plant availability. If jackrabbits are food-limited then a quantitative and/or qualitative food shortage should be observable in the field.

Development of Hypotheses

At this point it is necessary to operationally define the term availability. I defined available forage as forage that is present and usable to the organism. For jackrabbits this means all above ground herbage except woody material larger than the diameter of a pencil (7 mm). Woody stems larger than this are not readily consumed by browsing hares (Shoemaker et al. 1976, Windberg and Keith 1976).

Studies have shown that herbivores such as jackrabbits have food preferences, even though they are considered generalists. That is, they do not feed in proportion to the availability of the vegetation. Diet selection is thus an important component of the
plant-herbivore interaction. Westoby (1974) proposed an optimization hypothesis of forage selection in large generalist herbivores, using jackrabbits as a model. By using proximal cues and long-delay learning, the herbivore might be able to select a diet with an adequate mix of nutrients for the long-term, even in the face of changing availability. One prediction of this model constitutes the first testable hypothesis of the current study.

H(1): "The optimization model implies that their diet composition will not be affected by changes in availability as long as the major components of the diet occur at densities above about 10 kg/ha" (Westoby 1974:298).

The fact that herbivores do select their diet and that not everything above the ground is available suggests several possibilities with regard to food limitation at the population level. Populations may never become so dense that an adequate diet cannot be found and ingested by all the individuals. However, population densities may reach high enough levels such that the relative availability of the forage to the individuals is decreased and an adequate diet cannot be found. By estimating what is required by the population, it may be possible to determine whether such limitation could occur. Thus, another testable hypothesis is suggested.

H(2): Jackrabbits do not require more forage for normal population processes than is available to them at high densities.
If a shortage of some plant species occurs, jackrabbits may switch their intake to other, more available food, in an attempt to maintain adequate nutrition. Composition of the diet would change, although intake would be similar to the period before any change in availability occurred. Dietary composition would be different in high and low density situations. Since individual nutritional requirements are central to such changes in diet, one might expect different responses by groups of animals with different requirements. Differences in the diet might occur for example between breeding females and non-breeding adults. Two dietary composition hypotheses are proposed.

H(3): Average dietary composition is not significantly altered between high and low population density periods.

H(4): Among breeding adults, male and female dietary composition is the same.

Under resource limitations jackrabbits might be forced to sacrifice quantity of forage ingested while attempting to maintain dietary composition. Individuals may suffer either deficiencies in specific nutrients or in energy intake, resulting in different energy and protein balance in populations from different density regimes. Two predictions that express these differences and that can be tested are:

H(5): Nutritional balance (energy and protein) of lactating adult females is not significantly different at high and low density of jackrabbits.
H(6): Nutritional balance (energy and protein) of females entering the breeding season after the overwinter period is not significantly different at high and low density of jackrabbits.

The herbivore functional response to changing plant availability may also play an important role in the stability of the plant-herbivore system (Holling 1959, Noy-Meir 1975). If availability becomes low enough, consumption may drop, jeopardizing nutritional health. Such responses may be abrupt, occurring over a narrow range of availability, or gradual with little effect on consumption until very low levels of availability. At high density the functional response may buffer changes in relative availability of resources. A final prediction about jackrabbit response to vegetation is:

H(7): At high density, population dynamics are not sensitive to the form of the individual herbivore consumption function.

These hypotheses are consequences of forage limitation, framed in the rangeland-jackrabbit-livestock-coyote system. These hypotheses do not exhaust the predictions about the system, but are hypotheses for which adequate experiments could be designed and data collected.

The implication that follows from dietary changes in response to a changing food supply is that dietary insufficiencies and different nutritional balance occur. These factors must result in changing patterns of mortality of adults and especially of juveniles in order to fit with the empirical observations of the population. This
logical sequence represents a complex hypothesis itself, although not one testable in the fashion of those above.

**Research Approach**

To test the above hypotheses, I combined field measurements with simulation model results. Since Westoby (1973) collected dietary data during a population high in Curlew Valley, a comparison with a low density period (the present) was possible. In addition, he collected vegetation data on above ground biomass. These data, along with the data of the US/IBP Desert Biome Curlew Valley Validation Site allowed derivation of estimates of biomass similar to the operational definition of the present study.

The nutrition hypotheses proposed are not easily tested in the field for a number of reasons. These hypotheses involve complex dynamic relationships for which suitable experimental control is not possible and physiological measurements for which suitable techniques do not exist (see Heasley 1977). In addition, jackrabbit populations are presently at low densities and it is difficult to know when another peak population might occur. However, a simulation modeling approach is ideally suited for coping with the complexity and dynamic characteristics of these systems (Forrester 1961, Holling 1966). It enables one to conduct controlled experiments in situations where empirical control is impossible. The objective of such a modeling exercise is to examine system behavior, not to predict specific system
states (Caswell 1976). The construction of the simulation model quickly identifies key relationships and weaknesses in the data base.

Many researchers discount the utility of models on the assumption that we lack adequate data on which to base a model. In this instance, we have a well-defined knowledge of nutritional mechanisms and quantitative data on which to base a model. Both Forrester (1961) and Holling (1966) emphasize the role of feedback from empirical methods to modeling and vice versa. Testing hypotheses via simulation is valid, although it does not carry the weight of an empirical test. The model results conducted herein may be ultimately subjected to empirical tests in the field.

Table 1 summarizes the study hypotheses and the associated experimental tests.
Table 1. A summary of the study hypotheses and the experiments associated with them.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Experiment</th>
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<tbody>
<tr>
<td>H(1): Dietary composition unaffected by changes in availability above 10 kg/ha.</td>
<td>Field experiment: Measure dietary composition and relate these directly to available biomass of forage.</td>
</tr>
<tr>
<td>H(2): Jackrabbits do not require more forage than is available at high population densities.</td>
<td>Model experiment: Compare simulated amount of forage required for normal population processes with that available.</td>
</tr>
<tr>
<td>H(3): Average dietary composition is not significantly different at high and low densities.</td>
<td>Field experiment: Compare dietary composition between high (Westoby 1973) and low (present study) densities.</td>
</tr>
<tr>
<td>H(4): Average dietary composition is not significantly different between males and females during the breeding season.</td>
<td>Field experiment: Compare dietary composition between sexes.</td>
</tr>
<tr>
<td>H(5): Nutritional balance of lactating females is not significantly altered at high density.</td>
<td>Model experiment: Compare simulated energy and protein balances under high and low density conditions.</td>
</tr>
<tr>
<td>H(6): Nutritional balance of females entering the breeding season is not significantly altered at high density.</td>
<td>Model experiment: Compare simulated energy and protein balances under high and low density conditions.</td>
</tr>
<tr>
<td>H(7): At high density, population dynamics are not sensitive to consumption functional response.</td>
<td>Model experiment: Compare simulated population density under various forms of functional responses to available forage.</td>
</tr>
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FIELD METHODS

The field measurements were designed to: (1) answer questions about dietary changes occurring during a jackrabbit density cycle, and (2) make direct estimates of plant utilization.

Study Area

The Curlew Valley jackrabbit study area is in Box Elder County, northwestern Utah. Gross et al. (1974) give a complete description of topography, general climate and vegetation, including a location map of the rabbit study area.

Briefly, valley floor elevations range from 1585 m to 1280 m, sloping from north to south. A few isolated hills (maximum elevation about 1585 m) occur in the study area. The climate is characteristic of the Northern Desert Shrub Biome with annual precipitation ranging from 180 to 420 mm. Mean monthly temperatures range from a low of -7°C in January to a high of 23°C in July. Four major vegetation zones occur along the elevational gradient, including those dominated by Utah juniper (Juniperus osteosperma), big sagebrush (Artemisia tridentata), shadscale (Atriplex confertifolia) and greasewood (Sarcobatus vermiculatus). In addition, some areas of the valley have been planted to crested wheatgrass (Agropyron desertorum). Two semi-shrubby species, which often occur as monotypic stands of limited total area, are Nuttall saltbrush (Atriplex falcata) and winterfat (Ceratoides lanata) (Gross et al. 1974, Shinn et al. 1975).
Understory vegetation within these types includes a variety of annual and perennial grasses, forbs, and small shrubs. Cheatgrass (Bromus tectorum) is a ubiquitous annual grass. The most important perennial grasses are squirreltail (Sitanion hystrix), Sandberg bluegrass (Poa sandbergii), and Indian ricegrass (Oryzopsis hymenoides). The most abundant forbs are annuals, including Halogeton glomeratus and Bassia hyssopifolia, and the crucifers Lepidium perfoliatum and Descurainia spp. Two noteworthy shrubs are little rabbitbrush (Chrysothamnus viscidiflorus), found in nearly all vegetation types, and gray molly (Kochia americana), found primarily in association with shadscale and greasewood.

The studies described here were carried out within the area shown in Figure 1, mainly in the center of the study area described by Gross et al. (1974). The area is crossed by many unpaved roads along which jackrabbit collections were made. Two livestock exclosures were constructed and are shown in the figure as N and S. Also note the location of the US/IBP Desert Biome Curlew Validation Site and the crested wheatgrass seeding area surrounding it. Detailed abiotic and biotic measurements were made at the Biome Site from 1969 to 1976, making it a valuable reference point for both the field and modeling studies.

Dietary Data Collection

Rabbit collections

Jackrabbits were collected monthly in all months except August, September and December as part of the jackrabbit population studies.
Figure 1. The Curlew Valley jackrabbit study area. Unimproved roads are marked as dashed lines; the shaded areas designate those portions where most of the jackrabbits were collected. N and S mark the locations of the two livestock-proof exclosures used in the study.
(Gross et al. 1974, L. C. Stoddart, present principal investigator).
As much as possible, collections in 1976 were made from the same areas that Westoby (1973) studied during 1971-1972. However, due to low densities, other collecting areas were used to increase sample sizes. Rabbits were shot at night (roughly, dusk to 2400 hrs.), during the feeding period, along the unpaved roads. The areas where most of the rabbits were taken during 1976 are shown by shading in Figure 1. A flag was placed at each kill site and a record of the site made on a map for future plant-sampling reference. Stomachs were removed at the time of processing the carcasses (within 24 hrs., the contents removed, washed free of animal tissue and mucous over a 100 mesh (0.15 mm) screen, and frozen for later analysis. All stomach samples were labeled by sex, age, reproductive status and shooting location.

Stomach content analysis

The technique used for analysis of percentage dry weight composition of stomach contents was basically that of Sparks and Malechek (1968) as modified by Westoby (1973). Once the stomach contents were dried and ground in a Wiley mill, a small sample was removed for preparation of microscope slides. From the cleared and stained sample, two permanent slides were made. On each of the slides, 50 fields were selected systematically and examined at 100 power magnification for identifiable epidermal fragments. The relative density of each species (no. of particles of species A/total no. of particles identified x 100) was recorded as percent dry weight composition of the diet (Sparks and Malechek 1968).
Before any stomach content analysis could be done, a reference collection was required which included 60 species of plants collected in Curlew Valley at various phenological stages. Slides were made by the same procedures as above from whole samples and from samples separated by plant parts. An observer was trained using these reference slides. Once the observer felt confident, a series of 33 trials with known mixtures of varying composition was run using the exact procedures outlined above. A series of trials was then used to examine problems of misidentification, unidentifiability and bias of the technique and the observer.

Vegetation Availability Measurements

Estimating available biomass by individual species, for each sample of jackrabbits taken, was solved using a double sampling procedure (Cochran 1963). A large sample of cover, by species, was made after each jackrabbit collection. At the midpoint of the collecting seasons, January, April, July, and October, a smaller sample was taken in which both plant cover and biomass were measured. These two samples were combined as outlined below to estimate the dry biomass of each plant species available to the rabbits at their collection time.

The relationship between coverage and dry biomass is quite variable for some plant species and less so for others. Various measurements of plants have been used to estimate biomass, including stem diameter (Telfer 1969), foliage cover (Hutchings and Mason 1970), and crown volume (Bentley et al. 1970). Crown cover is a good index
of biomass for most species of grasses and forbs (Payne 1974), although a variable estimator of shrub biomass. Since crown cover is easily measured in the field, this measure was used to estimate dry biomass.

**Sampling plant cover**

**Sampling strata.** Rabbits were collected in all of the major vegetation types in Curlew Valley except juniper. The six types used in the vegetation analysis included the greasewood, shadscale, sagebrush, crested wheatgrass, and Nuttall saltbrush types already described. Another type designated annuals, consisted of disturbed areas with nearly 100 percent cover of annual forbs (mostly *Halogeton, Bassia*, and the crucifers). After each jackrabbit collection, shooting locations were located on aerial photographs. In many cases sites could be located quite accurately (within 50 m) because of easily recognized landmarks. In other cases locations were estimated from the vehicle odometer. A circle scaled to radius 300 m, which is approximately the radius of a jackrabbit's home range in Curlew Valley (Nelson 1970), was drawn on on the photographs around each collection site. A dot grid was used to estimate proportions of each vegetation type in the total area where rabbit collecting had taken place on that date. These proportions were used to weight the stratified plant cover samples taken.

**Sampling species cover within a type.** Cover measurements were taken within 1 week of the rabbit collection date, except for the July collection when they were taken within 2 weeks. Cover (cm$^2$ of plant/0.1 m$^2$) was measured for each species in 0.1 m$^2$ rectangular
frames. Frames of 1 m$^2$ or less are well adapted to semi-desert grassland and desert shrub types where cover is less than 100 percent (Daubenmire 1959). Three transects were randomly located within each vegetation type in which rabbits were collected. Each transect was a cluster of 40 systematically placed frames. Frames were placed every 3 m and at a 45° angle to the transect to avoid biases associated with maintaining a straight line of travel.

The transects were statistically treated as two stage cluster samples (see Cochran 1963:277-278). Mean cover for each species and its associated variance, was estimated by assuming that the first stage sampling fraction is negligible and thus ignoring the within transect variance (Cochran 1963:278).

Combining the stratified samples

The cover estimates for a species within a strata were combined to give a grand mean of cover over all of the vegetation types sampled on each shooting date. This was done by using the weighting proportions of each vegetation type sampled on that date (Cochran 1963:288). Air-dried weights are customarily used in biomass estimation work (Brown 1954), and dry weight estimates were needed for comparison with the stomach analyses results. For grasses, forbs and small shrubs, all vegetation above ground was clipped and weighed. For large shrubs, such as greasewood and big sagebrush, above ground material smaller than the diameter of a pencil (approximately 7 mm) was taken.

Linear regression of dry weight (g/0.1 m$^2$) with cover (cm$^2$/0.1 m$^2$) was run for each species at each season. Dry weight biomass available
Vegetation Utilization Measurements

Exclosure studies

In April 1976 two livestock-proof exclosures were constructed in Curlew Valley (see Figure 1) in which jackrabbit utilization of gray molly (Kochia) and squirreltail (Sitanion) was monitored. These plants were selected because of their importance in the diet and quality as jackrabbit forage (Westoby 1973). Variations in utilization of the fraction of total food that is of the highest quality may be important in linking food and populations (Moss et al. 1974, Stoddart et al. 1975). Each exclosure is a 1 ha square, with sides oriented parallel to the cardinal compass directions. The North exclosure is in the shadscale vegetation type while the South exclosure is in the greasewood type. The corners of 24 permanent, 2 x 8 m plots, were located randomly with respect to the northeast corner of each exclosure. All permanent plots have the long axis east to west.

Plot size was based on estimated plant density (from Westoby 1973, and preliminary samples, this study) and desired sample size for statistical comparisons (Hicks 1964:17). During the first two sampling periods plants of each species were randomly selected from within each plot at the time of sampling. Thereafter plot size was reduced to 2 x 2 m including a total sample of 200-300 plants.
Six sampling periods were used to estimate utilization from June 1976 to February 1978. Sampling was done at approximately peak standing crop for each species (usually June, Shinn et al. 1975) during late summer when plant water content is lowest (September, MacMahon et al. 1976), and in late winter (February). Estimates of individual plant biomass and utilization were made for each sampling period.

Utilization was defined as removal from the plant and thus included what was ingested by the herbivore and what was wasted. Jackrabbits are known to waste a fraction of some woody plants browsed, although they probably waste less of the easily ingested, palatable plants such as grasses (Currie and Goodwin 1966, Shoemaker et al. 1976). Cut stems of the wasted material were a cue for observers to detect browsing by jackrabbits. Litter was removed from around the browsed plants after an estimate had been made so that no confusion would result at the time of the next sample. Broken or torn stems were excluded from the utilized fraction and assumed to be litter. Black-tailed jackrabbits are the only Lepus species to occur in Curlew Valley. Two cottontail species (Sylvilagus nuttalli, Sylvilagus idahoensis) occur, but these are both restricted to habitats unlike the exclosure locations. Johnson (1961) surveyed the food habits of rodents in similar rangeland areas in Idaho and found only two species that might potentially have eaten grass (Reithrodonontomys megalotis, Lagurus curtatus). Neither of these species occur in habitats similar to the exclosure locations. None of the animals Johnson surveyed ate significant amounts of Kochia, although it occurred in his study area.
The ocular calibration technique (Brown 1954, Tadmor et al. 1975) was used to measure both biomass standing crop and average utilization per plant. Calibration trials were run each morning before observations were made on a particular species. An attempt was made during the calibration trials to simulate the way a jackrabbit might feed. Some clipped "wastage" was usually left next to the clipped plant and clipping was irregular. Plant size, wastage, and the size and number of stems clipped were used to estimate the proportion of the plant removed.

Calibration statistics were derived from linear regressions of actual biomass (or utilization) with the estimated values. Typically, 50 calibration plants were examined on each sampling date. After calibration, visual estimates of biomass and utilization per plant were made within the exclosures. The mean of visual estimates was converted to the best estimate of actual biomass or utilization using the calibration statistics (Tadmor et al. 1975:66, 68).

This measure of utilization is the mean percentage removal for only those plants that were utilized to some degree.

Another measure of utilization was also calculated from the same exclosure samples. This expression was simply the proportion of plants of the total sample that had some utilization (Stoddart et al. 1975). These estimates were made so that valley-wide samples could be compared to the exclosure estimates.

The above methods are likely in error to some unknown degree because wastage is variable, particularly for Sitanion, and some utilization probably went undetected. Also, production between
sampling periods could be removed and not detected. Since only new browsing (litter still green) was recorded as utilization, the method estimates the standing crop removed immediately prior to sampling.

Valley-wide estimates

In order to see if the utilization patterns were similar throughout the study area, samples of the proportion of Kochia plants utilized were taken at the same time as exclosure samples (June 1977, September 1977, February 1978). Approximately 20 square mile sections were randomly selected from the study area map for each sampling period. Searches for Kochia plants were made along the roads in these sections. At the first location found, 100 plants were sampled by the wandering quarter method (Catana 1963). The presence or absence of browsing was noted for each plant and from these valley-wide samples the proportion of plants showing some utilization was estimated.
MODELING METHODS

Model Objectives

Some of the nutritional questions to be answered were examined via simulation. A model was constructed based on data from the present field studies, previous field studies in Curlew Valley (Westoby 1973, Gross et al. 1974, Sotddart 1975, 1976, 1977), nutritional data from the literature and other models of bioenergetics and nutrition.

There are a wide range of herbivory models. Many of the published models used general energy metabolism structures to examine the role of consumption in ecosystems (Timin 1973, Rice et al. 1974). Other models have dealt in more detail with energy and other nutrient dynamics, similar to the emphasis of this modeling effort. The studies of Payne (1974), Wiens and Innis (1974), Heasley (1977) and the Grassland Simulation Model (Innis [ed.] 1978, in particular the mammalian consumer submodel of Anway 1978) were particularly influential in my model structure and analysis.

The goal of the modeling effort was to compare simulated jack-rabbit dynamics for years of high and low density. If diet is to affect jackrabbit nutrition and population dynamics, nutrient quality of the available forage seems as critical as the quantity. Therefore, protein and energy balance were chosen as indicators of nutritional health (Maynard and Loosli 1969). The model objective was selected that would focus the simulation studies along these lines:
What is the effect, on protein and energy balance in jackrabbits, of variations in diet, relative availability of preferred forages, and population density?

This objective was sufficiently detailed to guide model construction.

**Model Development**

The documentation method of Katzan (1976) was used because it allows each model component to be considered separately and presents model processes in a logical order. A variable dictionary and model listing appear in Appendices A and B.

**Jackrabbit experimental model**

A hierarchical diagram for the jackrabbit experimental model (JACRABIT) is shown in Figure 2. Its three basic components are the nutrition submodel (JACNU), the population submodel (RABBITS) and a stochastic parameter generator. Figure 3 shows the general input, process and output structure of the model. The model is formulated in difference equations and is written in FORTRAN IV for the Burroughs 6700 computer at Utah State University.

A stochastic parameter generator was included since it was desired that hypothesis tests made with the model be statistically valid. Statistical tests are not possible with a deterministic model, so JACRABIT can randomly select parameters before a run. The mean, standard deviation and source for each parameter is given in Appendix A. In cases where a range of values is reported, the range divided by four (Cochran 1963).
Figure 2. Hierarchical diagram of the jackrabbit experimental model.
JACRABIT 0.0

<table>
<thead>
<tr>
<th>INPUT</th>
<th>PROCESS</th>
<th>OUTPUT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Debugging and output controls</td>
<td>Generate final parameter values for the run (2.0)</td>
<td>Debugging values, output controls, length of simulation and time step</td>
</tr>
<tr>
<td>Length of simulation and time step</td>
<td>Determine nutritional balance, JACNU (1.0)</td>
<td>Final parameter values and initial conditions</td>
</tr>
<tr>
<td>Parameters and table functions (means and standard deviations)</td>
<td>Determine population changes, RABBITs (3.0)</td>
<td>Energy balance, protein balance, and body weight changes by sex and age class</td>
</tr>
<tr>
<td>Initial conditions for state variables</td>
<td></td>
<td>Natality, mortality values, and population density change</td>
</tr>
</tbody>
</table>

Figure 3. Overview diagram of the jackrabbit experimental model - JACRABIT.
is used as an estimate of the standard deviation. At the beginning of each model run a normal random number generator is called which randomly picks a final parameter value using the given mean and standard deviation. The parameter values are fixed for the duration of the run. Thus, two parameter sets are never identical and statistical comparisons can be made between output variables.

Nutrition submodel

The nutrition submodel considers the effects of energy and protein balance on weight changes of sex and age classes of jackrabbits. The Forrester (1961) diagram (Figure 4) shows the state variables which are the live weights of individuals. The simulation of live weight was chosen for two reasons:

(1) There is considerable evidence for a relationship between body weight, animal condition, and survival (Kleiber 1961, Klein 1970, Moen 1973, Moss et al. 1974, and Keith and Windberg 1978); and

(2) There are data on jackrabbit body weights (Stoddart 1972) from the Curlew Valley studies for model validation.

Model construction proceeded by integrating published energy and protein relationships. Symbols used in the model are defined in Appendix A. One of the basic ideas incorporated into the model is that large herbivores eat for energy. It is assumed that immediate food intake is controlled by energy balance and that forage selection balances other nutrients, like protein (Crampton and Harris 1969, Maynard and Loosli 1969). Metabolizable energy (ME, kcal/indiv./day) was summarized by Moen (1973) as:
Figure 4. Forrester diagram of the nutrition submodel. All symbols are defined in Appendix A.

*a* Litter group.
where, \[ \text{ME} = \text{NE}_p + \text{HP} \]

\[ \begin{align*}
\text{HP} &= \text{[Basal metabolic energy]} + \text{[Homeothermic energy]} \\
&\quad + \text{[Activity expenditure]} + \text{[Heat increment of food]}, \\
\text{and} \\
\text{NE}_p &= \text{[Tissue growth energy]} + \text{[Gestation energy]} + \text{[Lactation energy]}.
\end{align*} \]

Total nitrogen (for protein) used daily (TDNR, g N/indiv./day) is as follows (Moen 1973):

\[ \text{TDNR} = \text{[Metabolic nitrogen]} + \text{[Tissue growth nitrogen]} \\
&\quad + \text{[Gestation nitrogen]} + \text{[Lactation nitrogen]}. \]

These relationships form a basis for the nutrition submodel.

The inputs required for the nutritional submodel are shown in Figure 5, including those from the population submodel. The diagram also shows the sequence of processes modeling energy and protein requirements, forage intake, and nutritional balances producing body weight and condition exchanges. Each of the processes will be treated separately.

**Existence energy and protein requirements.** Existence energy and protein required are those needed for normal body maintenance and activity, exclusive of any production costs for growth or reproduction. The equations for the adult males are used to illustrate development of these requirements; other sex and age classes are done similarly.

Basal heat production (BHP) is calculated from the power law of Kleiber (1961) in subroutine HEAT. Basal heat production is
<table>
<thead>
<tr>
<th>INPUT</th>
<th>PROCESS</th>
<th>OUTPUT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yearly temperature parameters (2.0)</td>
<td>Determine existence energy and protein requirements</td>
<td>Total energy and protein requirements by sex and age class</td>
</tr>
<tr>
<td>Nutritional/physiological parameters, growth parameters and conversion efficiencies (2.0)</td>
<td>Determine energy and protein requirements for reproduction</td>
<td>Energy and protein balance by sex and age class (3.0)</td>
</tr>
<tr>
<td>Dietary composition and nutrient content of herbage, herbage availability.</td>
<td>Determine growth requirements for energy and protein</td>
<td>Daily milk production during the breeding season</td>
</tr>
<tr>
<td>Population values including reproductive data and density (3.0)</td>
<td>Determine forage intake</td>
<td>Body weight values by sex and age class (3.0)</td>
</tr>
<tr>
<td>Initial body weights for sex and age classes</td>
<td>Determine net energy and protein balance</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Determine body weight change for each sex and age class</td>
<td></td>
</tr>
</tbody>
</table>

Figure 5. Overview diagram of the nutrition submodel - JACNU.
modified by a term called heat production increment (HPINC) which simulates the energy cost of thermoregulation as a multiple of BHP. Air temperature is supplied by a stochastic generator with mean, standard deviation and amplitude parameters measured at the Desert Biome Validation Site (see Balph et al. 1974). HPINC is derived from the equations given by Hinds (1977) for metabolic rate of black-tailed jackrabbits measured by oxygen consumption at various temperatures. Since Hinds observed that jackrabbits acclimated to different temperature regimes seasonally, the model uses the values he derived for winter temperatures with a control parameter that switches to summer acclimatization at the appropriate time. Heat increment is the energy cost (multiple of BHP) for digestion of food. An average value of 0.40 was used based on Maynard and Loosli (1969) and Anway (1978).

Total heat production (THP, kcal/day) is then given by:

\[ \text{THP} = \text{BHP} \times (1 + \text{HPINC} + \text{AHI}) \]

where, \( \text{BHP} = \) basal heat production (kcal/day), \( \text{HPINC} = \) heat production increment (dimensionless), and \( \text{AHI} = \) average heat increment (dimensionless).

A value of 0.40 times basal heat production was used for general activity increment (GAINC) as suggested by Gessaman (1973) and Moen (1973). GAINC was modified according to sex and age class and season. For example, activity increment for adult males (AINCM) was 1.1 times GAINC since adult males were considered to be 1.1 times more active
than adult females, based on the telemetry data for black-tailed jack-rabbits of Nelson (1970) and Costa et al. (1976). Male activity increases even more during the breeding season (1.33 times GAINC, Haug 1969), especially during conception periods.

Young, prior to weaning, had reduced activity increment (AINCY) since their movements are thought to be slight during this period (Haskell and Reynolds 1947). Activity increases linearly until they attain full juvenile status, between 40 and 50 days, when the activity increment of juveniles (AINCJ) reached 1.33 times the GAINC. Activity increment of young from birth to age 42 days is given by:

\[
\begin{align*}
\text{AINCY} &= \text{GAINC} \times 1.0 \quad \text{AGE} \leq 7 \\
\text{AINCY} &= \text{GAINC} \times (0.93 + 0.01 \times \text{AGE}) \quad 7 < \text{AGE} \leq 42 \\
\text{AINCY} &= \text{GAINC} \times 1.33 \quad \text{AGE} > 42
\end{align*}
\]

Daily existence energy requirements of males (DERM, kcal/indiv./day) was calculated as

\[
\text{DERM} = \text{THP} + \text{BHP} \times \text{AINCM}.
\]

Existence protein requirements include only metabolic nitrogen costs, excluding growth and reproduction functions. For example, a male has only endogenous urinary nitrogen loss (EUN, g N/day) and metabolic fecal nitrogen loss (MFN, g N/day) for total daily nitrogen requirement (TDNRM). Moen (1973) gives

\[
\text{EUN} = \text{PP1} \times (\text{WWW})^{\text{PP2}},
\]
for estimating this loss: where,

\[ PPI = \text{weight specific nitrogen metabolism (0.146 gN/kg}^{0.75} \text{/day)}, \]
\[ WvW = \text{body weight (kg), and} \]
\[ PP2 = 0.75. \]

This loss represents maintenance and replacement of cells and structural proteins.

Metabolic fecal nitrogen (MFN) includes sloughed intestinal lining, enzymes, and other digestive losses. This loss is estimated by the form given by Moen (1973):

\[ MFN = (\text{CMFN} \times \text{RFOOD})/\text{RATPN} \]

where, \( \text{CMFN} \) = g crude protein lost/kg food eaten (5.0 g CP/kg), \( \text{RFOOD} \) = required food intake (kg/day), and \( \text{RATPN} \) = ratio of total protein to nitrogen in body (g CP/g N).

Total daily existence nitrogen requirements are the sum,

\( \text{TDNRM} = \text{EUN} + \text{MFN}, \)

which is converted to crude protein requirements on multiplication by \( \text{RATPN} \). Rabbits are coprophagus and while this reingestion of feces probably is most important in vitamin nutrition, it serves to increase the quality of the protein ingested (Thacker and Brandt 1955, Nagy et al. 1976). Using the data of Johnson and Maxwell (1966) for pikas, it is estimated that on average coprophagy could reduce the daily nitrogen requirement by 10 percent. Thus \( \text{TDNRM} \) was readjusted by this factor:
TDNRM = TDNRM \times (1. - \text{CORP}),

where, \text{CORP} = \text{proportion of daily nitrogen requirements reduced by coprophagy (dimensionless).}

Body growth energy and protein requirements. Once mammals reach maturity protein is required only for maintenance (Maynard and Loosli 1969). Dry body weight changes in adults are limited to changing amounts of fat.

Energy and protein requirements for growth of young and juveniles are estimated from curves that represent potential growth. These rates of growth are considered "potential" because they are taken from captive animals fed ad libitum. A curve was fitted to the data of Haskell and Reynolds (1947), which shows that immature jackrabbits grow in essentially linear fashion from birth through weaning and to about 70 days of age. The daily rate of growth was estimated as the slope of a least squares linear regression using the data up to day 70. After this the growth rate begins to decline until mature weight (approximately 2.1 kg) is reached at roughly 245 days. These data were fit with a natural growth function (Parton and Innis 1972), using the numerical fitting approach of Hooke and Jeeves (1961) and least squares error criteria. The maximum weight (WK = 2.1 kg) was fixed and the routine was used to estimate only the rate constant. The two growth rate equations may be summarized as follows to give the overall potential growth function of jackrabbits from birth to maturity:
YRATE = CY  \quad \text{AGE} < 70 \text{ days}

and,

\[ \text{JRATE} = \text{WK} \times \text{CJ} \times e^{-\text{CJ} \times \text{AGE}} \quad 70 \leq \text{AGE} \leq 245 \]

where,

YRATE = growth rate of young (kg/indiv. * day),
CY = growth rate constant of young (kg/indiv. * day),
JRATE = growth rate of juveniles (kg/indiv. * day),
WK = mature body weight (kg/indiv.), and
CJ = growth rate constant of juveniles (1/day).

Once the potential growth was determined for each litter, estimates were made of the associated energy and protein needs. Existence energy and protein requirements of non-adults were estimated with the same equations used for adults. Tissue growth requirements were added to existence requirements.

Energy requirements for tissue growth (TISER, kcal/indiv. * day) were estimated by the equation:

\[ \text{TISER} = \text{PWI} \times \text{GRER} \times \text{DRY} \]

where,

PWI = weight increment (kg/indiv. * day),
GRER = growth energy (kcal/kg), and
DRY = proportion of weight increase that was dry biomass (dimensionless).
Holter et al. (1974) measured GRER (8190 kcal/kg) in snowshoe hares. GRER represents tissue energy balance, including addition of both protein and fat to body substance.

Protein requirements for growth were estimated as a constant fraction of the weight gain as suggested by Moen (1973).

\[ \text{NG} = \text{PWI} \times \text{CNG} \]

where, 
- NG = nitrogen required for growth (g N/day),
- PWI = potential weight increment (kg/day), and
- CNG = ratio of nitrogen to body weight (g N/kg).

Reproduction energy and protein requirements. Adult female jackrabbits have additional nutritional costs for gestation and lactation. Of these two, lactation is the most nutritionally demanding (Moen 1973, Randolph et al. 1977). Both represent important links between nutritional and population processes.

Gestation energy requirement per fetus per day (GER) was estimated by partitioning total gestation energy requirement by the amount of fetal growth occurring in that day. Total gestation energy requirement was given by Brody (1945) as:

\[ \text{TGER} = \text{GP1} \times (\text{WPAR})^{\text{GP2}} \]

where, 
- TGER = gestation energy requirement (kcal/fetus),
- GP1 = weight specific energy requirement (kcal/kg\(^{1.2}\)).
WPAR = weight of fetus at parturition (kg), and
GP2 = 1.2.

Millar (1975) and Randolph et al. (1977) showed that gestation energy requirements are directly related to litter size. Therefore, gestation energy requirements are multiplied by the litter size to produce the energy required for the whole litter.

Potential growth curves of fetuses were developed from the data of Bookout (1964) and Haskell and Reynolds (1947). Gestation period was taken as 42 days (Gross et al. 1974). Growth of the fetuses is slow until about the last third of the gestation period, at which time it increases rapidly. A piece-wise linear function gave smaller least squares error than any non-linear forms tried for these data. This fetal growth rate function is as follows:

\[
\text{FRATE} = \begin{cases} 
C_1 & \text{FETAL AGE < 12 days,} \\
C_2 & \text{12 \leq FETAL AGE \leq 24 days, and} \\
C_3 & \text{FETAL AGE > 24 days.}
\end{cases}
\]

The C's are in kg/indiv. • day. Thus, potential fetal growth is estimated for any time to estimate GER.

The protein required by a pregnant female for fetal development (NP, g N/day) is a function of the nitrogen content of the fetus and the additional nitrogen metabolism of the pregnant female (Moen 1973):
\[ NP = \left( \frac{WFET \times BPF}{RATPN} \right) \times LITS \times PINC \]

where, \( WFET \) = weight of fetus (kg/indiv.),
\( BPF \) = body protein fraction (g CP/kg),
\( RATPN \) = ratio of body protein to N (g CP/g N),
\( LITS \) = litter size (no. fetuses), and
\( PINC \) = nitrogen "overhead" for pregnancy (dimensionless).

\( PINC \) is 1.2 (Crampton and Harris 1969), and accounts for the nitrogen required to maintain fetal support tissues, as well as the increased rate of nitrogen metabolism during pregnancy.

The energy required by the lactating female is directly related to the energy requirements of her offspring. Even though young jack-rabbits are precocial, they are completely dependent upon the female for at least the first 5 to 10 days (Haskell and Reynolds 1947). Weaning is simulated with the function:

\[
\begin{align*}
RD &= 1.0 \quad \text{AGE} < 7 \\
RD &= 1.54 - 0.077 \times \text{AGE} \quad 7 \leq \text{AGE} \leq 20 \\
RD &= 0.0 \quad \text{AGE} > 20
\end{align*}
\]

where, \( RD \) = proportion of daily energy requirements derived from milk (dimensionless), and
\( \text{AGE} \) = age (days).
As the proportion of the daily energy requirement derived from milk decreases, the young increase their intake of green forage to meet their daily energy needs. This reduces the milk demand on the female, and hence her lactation energy requirement (Hahn and Koldovsky 1966, Schmidt 1971). Daily energy requirement (DERL, kcal/day) for lactation is:

\[
DERL = \left( \frac{TDERY \times RD}{NEMLK} \right) \times LITS
\]

where, \( TDERY \) = daily energy requirement per young (kcal/indiv. \( \times \) day), \( NEMLK \) = net energy ratio in milk (dimensionless), and \( RD \) and \( LITS \) are as defined previously.

It is important to note that this energy requirement for lactation assumes that the offspring are growing at their potential rate (Schmidt 1971, Moen 1973). Adjustment in both the energy and protein expenditure is necessary if demand is excessive or intake is restricted. Such adjustments will be discussed with energy and protein balance.

Protein requirements for lactation are based on the nitrogen content of the milk produced with some associated overhead protein cost. Potential daily milk production (PDMP, g milk/day) is:

\[
PDMP = \frac{DERL}{GEMLK}
\]

where, \( GEMLK \) = energy content of milk (kcal/ g milk).
Then nitrogen requirements for milk production (NL, g N/day) are:

$$NL = PDMP \times FMN \times LINC$$

where, $FMN =$ nitrogen fraction of milk (g N/g milk), and $LINC =$ lactation nitrogen increment (dimensionless).

The lactation nitrogen increment is about 1.3 times the nitrogen content of the milk according to Moen (1973).

**Forage intake**. Forage intake is a function of the animals' energy and protein requirements, the nutritional content and digestibility of the forage, the rate of passage through the gut, and the availability of forage (Moen 1973). Competition and behavior may modify forage intake (Moen 1973, Janis 1976, Shoemaker et al. 1976). Nine diet categories in the model correspond to the major food items of Curlew Valley jackrabbits. Diet categories are given in Appendix C. Dietary composition matrices specify the proportion of the diet that comes from each category during a particular month. The data for high jackrabbit population density years were taken from Westoby (1973). Data for low density years came from the present study. Both input matrices of dietary proportions are given in Appendix C.

There are two nutrient content matrices; one for energy content (kcal/g) and one for the crude protein content (percent dry weight) of plants (Appendix C). Data for these matrices were taken directly from Desert Biome sources (West 1972, Balph et al. 1974, Shinn et al. ...
1975, MacMahon et al. 1976, and uncompiled data) and Westoby (1973). Where seasonal values were given, nutrient contents were assumed to be constant over the season or to follow nutrient dynamics of an ecologically similar species. A few crude protein values for Kochia were derived from a small sample of plants taken during the present study (see Appendix D).

Herbage availability matrices were derived for the same nine plant categories from the data of West (1972), Westoby (1973), Balph et al. (1974), and Shinn et al. (1975) for the high jackrabbit density years. Values of standing crop biomass of combined leaves, new growth and 10 percent of the old growth were used from these sources to approximate the availability as I defined it for shrubs. Data from the present study, as well as MacMahon et al. (1976) and other uncompiled Desert Biome data, were used to derive the availability data for low density years. Westoby (1973) and the present study were the major data sources for the herbage availability matrices and were only supplemented from the other sources where omissions occurred. If a food category is insufficient to supply the demand from that category, the model switches consumption to the next most preferred category. For example, if the standing crop of Kochia was insufficient on a given day, the remainder of the Kochia consumption is taken from the Atriplex falcata.

Digestible and metabolizable energy coefficients were taken from the measurements on jackrabbits in the Mojave desert of Shoemaker et al. (1976) and crude protein digestibilities were taken from
Nagy et al. (1976) from the same studies. The metabolizable energy (MEDIET, kcal/g dry weight) is:

\[
\text{MEDIET} = \text{UE} \times \text{DIG} \times \text{GEDIET}
\]

where, \(\text{UE} = \) ratio of metabolizable to digestible energy (dimensionless),
\(\text{DIG} = \) digestible energy coefficient (dimensionless), and
\(\text{GEDIET} = \) gross energy of the diet (kcal/g dry weight).

Forage required each day (RFD, g dry weight/day) is then:

\[
\text{RFD} = \frac{\text{TDER}}{\text{MEDIET}}
\]

where, \(\text{TDER} = \) total daily energy requirement (kcal/day).

Food intake is influenced by changes in intake associated with breeding activities and behavior. It is well known that females' intake increases during pregnancy and especially during lactation (Hadjpieris and Holmes 1966, Randolph et al. 1977). It is also likely that males' intake decreases during the breeding season (Haug 1969). Voluntary food intake is often restricted by the water content of the forage because high intake would result in water balance problems (Nagy et al. 1976, Shoemaker et al. 1976). These changes in intake are simulated by step functions in the model which take values on the order of 1 to 2 percent of required forage intake (RFD).
Forage intake is also limited by the rate of passage through the gut. Shoemaker et al. (1976) estimated that jackrabbits feeding on coarse winter diets eat about 215 g dry food per day. The maximum dry weights of stomach contents collected during this study was 150 g but this represents only part of a 24 hours period.

Bailey (1969) said digestion in cottontails was such that an additional 65 percent of the stomach capacity could be ingested during 24 hours. Shoemaker et al. (1976) state that about half the feces produced in a night are from food consumed that night. Taking the rates of passage of Bailey and Shoemaker et al., I derived maximum consumption values for 24 hours (CMAX) of 248 to 300 g/day. I weighted the empirical estimate (Shoemaker et al. 1976) more heavily than the others and set CMAX at 240 g/day in the simulations presented.

Consumption is modified by herbage composition, demand, and by herbage availability. Consumption is modified by herbage availability (Westoby 1974, Noy-Meir 1975), as shown in Figure 6. It is logical that consumption must drop to zero at zero available herbage. It is not clear what functional form is appropriate. Noy-Meir (1975) cites examples of functional responses for predators and herbivores, and gives some empirical data for sheep. Westoby (1974) derived a function from data on sheep but suggested that it might hold for many large generalist herbivores, including jackrabbits.

The curves presented by Noy-Meir (1975) suggest that consumption for range sheep is maximum above 1000 kg/ha. Sheep consume 4 or 5 times as much herbage as jackrabbits in a 24 hour period. I assumed that jackrabbits reach maximum consumption at approximately 200 kg/ha. Four functional forms (ramp, Michaelis-Menton
Available herbage biomass (kg/ha)

Figure 6. Functional forms for changes in individual consumption rate with changes in available herbage; (a) linear to satiation, (b) gradual satiation, (c) sigmoid (adapted from Noy-Meir 1975).
Von Bertalanffy, and logistic; Parton and Innis 1972) were parameterized for input into the nutrition model. Since the functions are based on untested assumptions, parameter values are assigned large coefficients of variation (200-300 percent). As a result maximum consumption may be reached over a wide range of available herbage values, from 100 to 1000 kg/ha.

Net energy and protein balance. Once intake of protein and energy is determined, energy (EB kcal/day) and protein (PB, g protein/day) balance are calculated. Energy balance is calculated as:

$$EB = ME - TDER$$

where, $ME = \text{metabolizable energy assimilated (kcal/day)}$, and $TDER = \text{total daily energy requirements (kcal/day)}$.

Protein balance is calculated as:

$$PB = CPIN - DCPR$$

where, $CPIN = \text{crude protein assimilated (g protein/day)}$, and $DCPR = \text{daily crude protein requirement (g protein/day)}$.

Nutritional/physiological responses for different energy and protein balances are shown in Tables 2, 3, and 4. These tables summarize model readjustments to bring the animal into energy or protein balance. Zero balance is represented in the model as a narrow
Table 2. Adult male nutritional/physiological responses.

<table>
<thead>
<tr>
<th>Protein balance state (PB)</th>
<th>Energy balance state (EB)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Negative</td>
<td>Zero</td>
</tr>
</tbody>
</table>
Table 3. Adult female nutritional/physiological responses.

<table>
<thead>
<tr>
<th>Protein balance state (PB)</th>
<th>Energy balance state (EB)</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Negative</strong></td>
<td><strong>Zero</strong></td>
<td><strong>Positive</strong></td>
</tr>
<tr>
<td><strong>Zero</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Positive</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Protein catabolized for energy (Kleiber 1961).</td>
<td>1. No reductions necessary.</td>
<td>1. No reductions necessary.</td>
</tr>
</tbody>
</table>
Table 4. Young and juvenile nutritional/physiological responses.

<table>
<thead>
<tr>
<th>Protein balance state (PB)</th>
<th>Energy balance state (EB)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Negative</td>
</tr>
</tbody>
</table>
range (BAL, 0.1 kcal/day) around zero. This approach accounts for the fact that very small imbalances would not result in measurable changes in the animals.

For adult males the model mechanisms transform any shortage into body weight changes. For example, if the animal is in zero protein balance but negative energy balance, fat is catabolized to make up the deficit. The male's rate of body weight change (BRATE, kg/day) is:

\[
BRATE = \frac{EBM \times CAT}{EFAT \times DRY}
\]

where,

- \( EBM \) = energy balance of males (kcal/day),
- \( CAT \) = efficiency of fat catabolism (dimensionless),
- \( EFAT \) = energy content of fat (kcal/kg), and
- \( DRY \) = body dry weight fraction (dimensionless).

Adult females have the most complicated response mechanisms of any group in the model because of the variety of responses for a pregnant and/or lactating animal. In most mammals milk production is highly variable even within a single lactation. Reid (1963) points out that most maternal undernourishment can be corrected by reducing milk production. Females retain their own reserves at the expense of offspring (Randolph et al. 1977). When a modeled pregnant and lactating female is in negative protein or energy balance it first reduces expenditures for the reproductive functions. This reduction
is proportional to its requirement for each function resulting in some reduction in both gestation and lactation.

For example, if the female has sufficient protein but is in negative energy balance, the reproductive labile energy (ELAB, kcal/day) is partitioned into the proportion for gestation and lactation respectively.

\[
\text{ELAB} = \text{GER} + \text{DERL}
\]

then,

\[
E_1 = \frac{\text{GER}}{\text{ELAB}} \quad \text{and} \quad E_2 = \frac{\text{DERL}}{\text{ELAB}}
\]

are the dimensionless reduction fractions.

The reduction in energy expenditure (TOTRED, kcal/day) is calculated as a function of the energy balance (EBF, kcal/day), decreased by a fraction supplied from body stores (STOR, dimensionless).

\[
\text{TOTRED} = |\text{EBF}| - |\text{EBF}| \times \text{STOR}
\]

where, \( \text{ABS} = \) absolute value function.

Finally, the amount of energy by which each of the reproduction functions is reduced is given by:

\[
\text{GESRED} = \text{TOTRED} \times E_1 \quad \text{and} \quad \text{LACRED} = \text{TOTRED} \times E_2
\]
where, \( \text{GESRED} = \) gestation energy reduction (kcal/day), and \( \text{LACRED} = \) lactation energy reduction (kcal/day).

Body weight loss, related to the amount of energy taken from body stores, also occurs. The reduced amount of energy results in slower fetal growth and lower milk production.

This formulation produces results similar to published information. Since lactation energy requirements are many times greater than those for gestation, most of the negative energy balance will be accommodated by LACRED, resulting in lower milk yield. Only during the later part of pregnancy are gestation energy requirements of much consequence. Body weight losses are slight for most negative values of energy balance because the parameter \( STOR \) is set at 0.15.

When lactating females are protein deficient, the protein content of the milk is reduced. Data of Mueller and Sadlier (1977) for deer show a 1 percent reduction in milk protein during lactation is possible. A daily rate of milk nitrogen reduction was calculated based on these data and applied to the milk composition when the female is protein deficient.

When females have excess energy, it is stored at body fat (Randolph et al. 1977). Excess protein cannot be stored and is metabolized away (Maynard and Loosli 1969). Female body weight changes during the breeding season parallel these periods of accumulation and storage and subsequent catabolism.

Nutritional/physiological responses of young and juveniles are conceptually different from those for adults because of growth.
requirements. If energy or protein intake is restricted, growth continues but more slowly (Brody 1945). Only severe nutrient limitations will stop growth (Wilson and Osbourn 1960, Hahn and Koldovsky 1966, Chow and Rider 1973).

Young, nursing jackrabbits are dependent upon the female for nutrition, so deficiencies for the adult influence the young. As weaning occurs, the young begin to take a larger fraction of their nutrition from green feed and this may allow rapid increase in growth (Wilson and Osbourn 1960, Hahn and Koldovsky 1966, Barnes et al. 1973).

Nutritional impacts to young and juveniles are calculated like that of adults. If nutritional balances are negative, reductions in growth rates for both young and juvenile are calculated. The equation for juveniles (identical to that for young) under energy restrictions is:

\[ ERJF = (1. - \frac{ABS(EBJ)}{TDERJ}) \]

where,\n
- \( ERJF \) = energy reduction factor, juveniles (dimensionless),
- \( EBJ \) = energy balance of juvenile (kcal/day), and
- \( TDERJ \) = total daily energy requirement of juveniles (kcal/day).

Protein reduction factors are calculated similarly. These factors are then multiplied with the potential growth rates calculated. If both energy and protein are limited, the product of the reduction factors \( PRJF \) and \( ERJF \) multiplies the potential growth rate to simulate growth rate.
Body weight changes. The difference equation for all body weight state variable changes is:

\[ W(T + DT) = W(T) + DT \times RATE \]

where, RATE is calculated as described above.

Population submodel

The population submodel is less detailed than the nutrition submodel because less detail was needed to meet objectives. The submodel considers the effects of natality and mortality changes on the density of the various sex and age classes in the population. The state variables (Figure 7) are densities of individuals. Density is the number of individuals per hectare so that forage requirements are readily compared to available herbage.

Submodel construction relied on the hare demographic work of Gross et al. (1974), Stoddart (1975, 1976, 1977) and Keith and Windberg (1978). Terms are defined in Appendix A. The model assumes that the important demographic responses are associated with variation in mortality rates and that changes in natality have minor effects on density trends (Gross et al. 1974, Stoddart 1977). Mortality rates depend on predation by coyotes (Wagner and Stoddart 1972) and on unknown factors (Stoddart 1975). Mortality was, therefore, modeled as a function of predation and nutrition related mortality. This allows examination of the relative importance of nutritional deficiencies and predation on the population.
Figure 7. Forrester diagram of the population submodel. All symbols are defined in Appendix A.
The inputs required for the population submodel are shown in Figure 8, including those from the nutrition submodel.

**Natality.** Net natality is the number of ova implanted per female during each littering period. The litter size and the timing of pregnancies interact with the female's nutritional status. Average conception dates (TCON), which were taken from Gross et al. (1974) and Stoddart (1975, 1976, 1977) are input and average parturition dates (TPART) are calculated from conception dates and gestation period (GEST, 42 days) (Haskell and Reynolds 1947, Gross et al. 1974). Conceptions and parturitions are assumed to occur on the average date. Litter size (LITS) is input as average number of ova per female conceiving in a littering period. However, after conception, litter size (implanted fetuses/female) is time varying as a result of intrauterine mortality of fetuses. The proportion of females conceiving (PREG) is input and recruitment of fetuses RCFET (indiv./ha):

\[
RCFET = DADF(T) \times PREG(NLIT) \times LITS(NLIT)
\]

where,

- \( DADF(T) \) = density of adult females (indiv./ha),
- \( PREG(NLIT) \) = proportion of adult females conceiving in a littering period (dim.), and
- \( LITS(NLIT) \) = ova per adult female in a littering period (ova/indiv.).
### RABBITS 3.0

<table>
<thead>
<tr>
<th>INPUT</th>
<th>PROCESS</th>
<th>OUTPUT</th>
</tr>
</thead>
<tbody>
<tr>
<td>Conception dates, pregnancy rates, litter size, timing parameters (2.0)</td>
<td>Determine final pregnancy rate, parturition dates, litter size, and net natality</td>
<td>Natality additions to the population</td>
</tr>
<tr>
<td>Nutritional values including energy and protein balance (1.0)</td>
<td>Determine predation caused mortality rate and nutritionally caused mortality rate</td>
<td>Mortality losses due to nutritional problems and predation (1.0)</td>
</tr>
<tr>
<td>Predation rate, data and timing parameters</td>
<td>Combine mortality to determine net mortality</td>
<td>Density of subadults and adults, sex ratio, age ratio (1.0)</td>
</tr>
<tr>
<td></td>
<td>Determine density change of all sex and age classes</td>
<td></td>
</tr>
</tbody>
</table>

Figure 8. Overview diagram of population submodel - RABBITS.
Conception by juveniles is ignored in the current model. Breeding by first litter juveniles does sometimes occur in black-tailed jackrabbit populations but is a minor influence on demographics (Gross et al. 1974). Juvenile conceptions did not occur in the years of principal interest to model experimentation (1972 and 1976).

Predation and natural mortality. Average instantaneous mortality rates were taken from the regression relationships given by Stoddart (1977). These rates are functions of predation level and the intercept is an estimate of natural mortality \((\text{NAT})\) in the absence of predation. Survival is modified by the nutritional condition of each life history stage. Energy and protein deficiency ratios \((\text{EDU} \text{ and } \text{PDU})\) represent nutritional condition. These are:

\[
\text{EDU} = \frac{(\text{EB} + \text{TDER})}{\text{DER}}
\]

and\[
\text{PDU} = \frac{\text{CPIN}}{\text{DCPR}}
\]

where, all variables are as defined previously.

The deficiency unit \((\text{DU})\) for each age class is then taken as the minimum of \(\text{EDU}\) and \(\text{PDU}\) to represent the limiting factor. A DU equal to or greater than one represents no deficiency.

Deficiency units modify survivals according to a survival fraction function \((\text{SFRAC}, \text{Figure 9})\) of logistic form (Heasley 1977). Parameters were chosen so that \(\text{SFRAC} = 1\) when \(\text{DU} = 1\). Parameter \(\text{SF1}\) is 1.05 so that survival can be increased as well as decreased. Daily survival rate \((\text{SNAT})\) is the \(n\)th root of the survival rate for the life history period:
Figure 9. Survival function (SFRAC) as a function of deficiency units (DU).

\[ SFRAC = \frac{SF1}{1 + SF2 \times \exp(-SF3 \times DU)} \]
SNAT = (SCJM)^1/CJMN

This daily rate is modified by daily nutritional balance variables to simulate changes in survival as a function of deficiencies.

SNAT = SNAT \times SFRAC (DU, SF1, SF2, SF3).

Natural mortality is treated similarly for adult males and females. Stoddart (1977) separated seasonal mortality into two periods; November to March (winter) and April to October (summer). Subadult and adult mortality over winter is the same, but from birth to October, juvenile mortality is treated separately (Stoddart 1975). This model separates the subadult rate into two life history stages; young (from birth to weaning) and juveniles (from weaning to October). This mechanism allows separate simulation of mortality during these life history periods, which are nutritionally very different.

Combining natural and predation mortality. Model functions act on the input potential mortality rates and these are combined to give the final mortality rate. The model calculates average mortality as a function of predation and environmental conditions. The instantaneous mortality rates are additive (Ricker 1975, Anderson and Burnham 1976). The survival rate (ST, density/density) is:

\[ ST = e^{-(NAT + PRD)} \]

where, \( PRD \) = predation mortality rate (density/density), and \( NAT \) = natural mortality rate (density/density).
Daily mortality rate (MORT, 1/days) is given by:

\[
MORT = \frac{1 - (ST)^{1/CJMN}}{DT}
\]

where, \( CJMN = \) number of time steps in the life history period, and \( DT = \) length of time step (days).

**Determining density change.** Except for recruitment of fetuses and young (discussed above under natality determination), all density changes are the result of mortality of a cohort. Mortality rates are relative so flow rates are (using males as an example):

\[
DBFLO = -AMMORT \times DADM
\]

where, \( DBFLO = \) density loss rate (no./ha * days), \( AMMORT = \) daily mortality rate function (1/days), and \( DADM = \) density of adult males (no./ha).

Level changes are then:

\[
DADM(T + DT) = DADM(T) + DT \times DBFLO
\]

where, \( DADM(T + DT) = \) density of adult males in the next time interval (no./ha).

All sex and age classes are handled similarly.
Model Verification, Validation and Sensitivity

Verification and validation consist of conducting tests to increase the assurance of the model's adequacy in meeting the objectives, and to evaluate its accuracy and the range of conditions over which it is useful (Caswell 1976). Verification involves checking the mathematical representation of hypotheses and checking to be sure the computer code represents the mathematical formulations. Validation involves comparing model output with observations of the real system behavior.

Data on variation in body weights (Stoddart 1972) were used to validate the nutrition submodel. Data from 1962 and 1963 were used to build the model and data from 1964-1967 were then used in validation. Validation criteria required that model results fall within the 95 percent confidence limits on the data, 80 percent of the time.

Other forms of validation included checking for reasonableness, completeness and running the model with random parameter sets to investigate model robustness. No statistical confidence limits were included by Gross et al. (1974) and Stoddart (1975, 1976, 1977) for validation tests of the population submodel.

Sensitivity analyses expose errors, identify sensitive parameters, and are good for corroborating model structure (Caswell 1976). Parameters were selected in each submodel and altered by varying amounts. Changes in model output variables were summarized as the ratio of output change to parameter change,
Sensitivity indicator = \[
\frac{\text{fraction change, output}}{\text{fraction change, parameter}}.
\]

All modeling testing was completed before model experiments were conducted.

**Model Experimentation**

Two approaches to model experimentation were taken; one testing "biological significance," the other testing "statistical significance." "Biological significance" tests are evaluations of model results using our intuition about the biological system. Model tests of "biological significance" do not allow the assignment of specific probabilities to the result, but yield some sense of the likelihood of a given result. For example, to the test H(5) comparing nutritional balance during high and low density periods, simulation with the low density population inputs was used as a control. A simulation using the high density inputs was compared to the control run with respect to energy and protein balance of females (EBF and PBF) during lactation. Next, a series of simulations were made with progressive changes made in parameters which are well known biologically (e.g., digestive efficiency ratios, DIG), until the same differences were produced as those produced by the different density inputs. Then a conclusion was drawn about the likelihood of the population density effect using biological intuition about the likelihood of the changes in digestibility.

The other kind of model tests are the familiar tests of "statistical significance." Tests of "statistical significance" use stochastic
parameter sets allowing model results to be compared by analysis of variance. For example, statistical tests were made when examining H(5) in a 2 x 2 factorial design (Hicks 1964:95-99). The number of runs necessary for 95 percent confidence was determined after estimating variability in the output from preliminary runs (Hicks 1964:16).

Many simulations made during the course of model experimentation were not designed to examine a hypothesis but simply gave some indication of system behavior. The examination of system dynamic characteristics rather than specific system states gives insight into the biological system being simulated (Forrester 1961, Caswell 1976).
RESULTS OF FIELD STUDIES

Herbage Availability

Plant species coverage

Mean plant species coverage (cm²/0.1 m²) is presented in Table 5 for all rabbit sampling locations excluding those near the crested wheatgrass seeding. Standard errors indicate that coverage was highly variable, with coefficients of variation commonly exceeding 100 percent.

Coverage ranged from less than 1 percent for some rare species, to nearly 75 percent for some widespread annuals. Total coverage may exceed 100 percent because of canopy overlap. A rough indication of total community coverage may be achieved by examining the coverage of the dominant shrubs, since many other species grow beneath these shrubs. Dominant shrubs covered from 5 to 50 percent of the area, well within the range for such desert shrub types reported by Daubenmire (1959) and Uresk (1978). Note that Table 5 represents a composite for the whole shooting area and not all species would occur at each location. Species' estimates of coverage compare favorably with measurements made on the nearby IBP Validation Site (Balph et al. 1974).

Coverage of certain species was difficult to estimate, notably rare forbs (Sphaeralcea sp., Penstemon sp.), half-shrubs (Kochia americana), and annuals (Halogeton glomeratus and Bromus tectorum).
Table 5. Mean and standard error values for plant species coverage (cm²/0.1 m²) along the shooting route for all rabbits shot away from the crested wheatgrass seedings.

<table>
<thead>
<tr>
<th>Herbage type</th>
<th>Winter</th>
<th>Spring</th>
<th>Summer</th>
<th>Fall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sarcobatus vermiculatus</td>
<td>166 ± 135</td>
<td>421 ± 214</td>
<td>438 ± 178</td>
<td>475 ± 176</td>
</tr>
<tr>
<td>Atriplex confertifolia</td>
<td>203 ± 250</td>
<td>435 ± 173</td>
<td>198 ± 93</td>
<td>54 ± 20</td>
</tr>
<tr>
<td>Artemisia tridentata</td>
<td>8 ± 6</td>
<td>107 ± 89</td>
<td>226 ± 97</td>
<td>91 ± 35</td>
</tr>
<tr>
<td>Chrysothamnus spp.</td>
<td>2 ± 1</td>
<td>5 ± 4</td>
<td>15 ± 7</td>
<td>11 ± 6</td>
</tr>
<tr>
<td>Kochia americana</td>
<td>208 ± 40</td>
<td>188 ± 150</td>
<td>5 ± 3</td>
<td>360 ± 150</td>
</tr>
<tr>
<td>Atriplex falcata</td>
<td>7 ± 1</td>
<td>16 ± 8</td>
<td>21 ± 9</td>
<td>50 ± 18</td>
</tr>
<tr>
<td>Sitanion hystrix</td>
<td>157 ± 357</td>
<td>623 ± 304</td>
<td>586 ± 267</td>
<td>121 ± 65</td>
</tr>
<tr>
<td>Bromus tectorum</td>
<td>37 ± 15</td>
<td>37 ± 15</td>
<td>37 ± 15</td>
<td>37 ± 15</td>
</tr>
<tr>
<td>Other grasses</td>
<td>197 ± 201</td>
<td>87 ± 90</td>
<td>28 ± 6</td>
<td>598 ± 208</td>
</tr>
<tr>
<td>Halogeton glomeratus</td>
<td>1 ± 1</td>
<td>320 ± 125</td>
<td>271 ± 215</td>
<td>404 ± 393</td>
</tr>
<tr>
<td>Bassia hyssopifolia</td>
<td>112 ± 25</td>
<td>112 ± 25</td>
<td>112 ± 25</td>
<td>112 ± 25</td>
</tr>
<tr>
<td>Descurainia spp.</td>
<td>89 ± 22</td>
<td>128 ± 93</td>
<td>128 ± 93</td>
<td>128 ± 93</td>
</tr>
<tr>
<td>Lepidium perfoliatum</td>
<td>2 ± 1</td>
<td>2 ± 1</td>
<td>2 ± 1</td>
<td>2 ± 1</td>
</tr>
<tr>
<td>Other forbs</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Coverage for these annuals was the extent of a patch. Since the objective was to measure available biomass, this presents no serious problem as long as definition of coverage for a species was consistent throughout the double sampling.

Coverage and biomass relationships

Parameters of linear regression equations of dry weight (g/0.1 m²) with coverage are presented in Table 6. Examination of Table 6 indicates that parameters are not always different between seasons. For example, the slope parameter (b) for Sarcobatus changes little over the four seasons, indicating that the ratio of dry biomass to canopy coverage did not change much with season. This might be expected with a woody shrub such as Sarcobatus since much of the dry biomass is woody material. Other species, such as Sitanion hystrix, had much more seasonal variation in the ratio. These changes were probably due to changes in moisture content between seasons. In any case, seasonal regressions were applied in the calculation of herbage availability.

The coefficients of determination (r²) and the standard errors (s_{d,c}) shown in the table indicate that predictability was generally reasonable. Biomass for some species (notably the widespread annuals) was poorly predicted, however and resulted in more variable estimates of availability of these species.

These results compare favorably with other attempts to predict biomass from coverage. Payne (1974) developed regressions for predicting biomass from coverage for some grasses and forbs with r²
Table 6. Parameters of linear regression equations of herbage dry weight (g/0.1 m²) with canopy coverage (cm²/0.1 m²). These equations were part of the double sampling design to estimate total available biomass in the shooting area.

<table>
<thead>
<tr>
<th>Season</th>
<th>Species</th>
<th>Sample size</th>
<th>Slope (b)</th>
<th>Mean dry weight (g)</th>
<th>Standard error (sd.c)</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>Sarcobatus vermiculatus</td>
<td>24</td>
<td>0.031</td>
<td>16.8</td>
<td>3.569</td>
<td>0.851</td>
</tr>
<tr>
<td></td>
<td>Atriplex confertilolia</td>
<td>24</td>
<td>0.085</td>
<td>25.3</td>
<td>3.443</td>
<td>0.862</td>
</tr>
<tr>
<td></td>
<td>Artemisia tridentata</td>
<td>24</td>
<td>0.063</td>
<td>15.9</td>
<td>3.547</td>
<td>0.927</td>
</tr>
<tr>
<td></td>
<td>Chrysothamnus viscidiflorus</td>
<td>24</td>
<td>0.121</td>
<td>8.3</td>
<td>2.527</td>
<td>0.919</td>
</tr>
<tr>
<td></td>
<td>Kochia americana</td>
<td>24</td>
<td>0.066</td>
<td>29.8</td>
<td>3.264</td>
<td>0.925</td>
</tr>
<tr>
<td></td>
<td>Atriplex falcata</td>
<td>24</td>
<td>0.025</td>
<td>5.7</td>
<td>0.308</td>
<td>0.984</td>
</tr>
<tr>
<td></td>
<td>Sitanion hystrix</td>
<td>24</td>
<td>0.081</td>
<td>17.3</td>
<td>0.965</td>
<td>0.863</td>
</tr>
<tr>
<td></td>
<td>Halogeton glomeratus</td>
<td>24</td>
<td>0.066</td>
<td>13.3</td>
<td>4.896</td>
<td>0.779</td>
</tr>
<tr>
<td></td>
<td>Bassia hyssopifolia</td>
<td>24</td>
<td>0.032</td>
<td>6.7</td>
<td>1.812</td>
<td>0.904</td>
</tr>
<tr>
<td>Spring</td>
<td>Sarcobatus vermiculatus</td>
<td>30</td>
<td>0.025</td>
<td>82.8</td>
<td>47.328</td>
<td>0.664</td>
</tr>
<tr>
<td></td>
<td>Atriplex confertilolia</td>
<td>30</td>
<td>0.056</td>
<td>62.1</td>
<td>22.527</td>
<td>0.829</td>
</tr>
<tr>
<td></td>
<td>Artemisia tridentata</td>
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<td>0.060</td>
<td>16.0</td>
<td>0.983</td>
<td>0.967</td>
</tr>
<tr>
<td></td>
<td>Chrysothamnus viscidiflorus</td>
<td>30</td>
<td>0.020</td>
<td>10.4</td>
<td>7.667</td>
<td>0.933</td>
</tr>
<tr>
<td></td>
<td>Kochia americana</td>
<td>30</td>
<td>0.017</td>
<td>7.3</td>
<td>2.564</td>
<td>0.734</td>
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<td>Atriplex falcata</td>
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<td>0.075</td>
<td>5.4</td>
<td>3.306</td>
<td>0.921</td>
</tr>
<tr>
<td></td>
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<td>30</td>
<td>0.021</td>
<td>11.3</td>
<td>3.976</td>
<td>0.668</td>
</tr>
<tr>
<td></td>
<td>Agropyron desertorum</td>
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<td>0.030</td>
<td>14.4</td>
<td>7.654</td>
<td>0.750</td>
</tr>
<tr>
<td></td>
<td>Bromus tectorum</td>
<td>24</td>
<td>0.047</td>
<td>7.6</td>
<td>7.001</td>
<td>0.349</td>
</tr>
<tr>
<td></td>
<td>Halogeton glomeratus</td>
<td>30</td>
<td>0.012</td>
<td>12.4</td>
<td>12.111</td>
<td>0.755</td>
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<tr>
<td></td>
<td>Bassia hyssopifolia</td>
<td>24</td>
<td>0.015</td>
<td>12.7</td>
<td>9.667</td>
<td>0.798</td>
</tr>
<tr>
<td>Summer</td>
<td>Sarcobatus vermiculatus</td>
<td>30</td>
<td>0.033</td>
<td>30.3</td>
<td>18.896</td>
<td>0.767</td>
</tr>
<tr>
<td></td>
<td>Atriplex confertilolia</td>
<td>30</td>
<td>0.058</td>
<td>56.1</td>
<td>14.396</td>
<td>0.296</td>
</tr>
<tr>
<td></td>
<td>Artemisia tridentata</td>
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<td>0.057</td>
<td>31.7</td>
<td>14.006</td>
<td>0.631</td>
</tr>
<tr>
<td></td>
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<td>0.027</td>
<td>12.4</td>
<td>4.598</td>
<td>0.868</td>
</tr>
<tr>
<td></td>
<td>Chrysothamnus nauseosus</td>
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<td>0.046</td>
<td>21.3</td>
<td>9.940</td>
<td>0.873</td>
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<tr>
<td></td>
<td>Kochia americana</td>
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<td>0.040</td>
<td>14.4</td>
<td>4.652</td>
<td>0.261</td>
</tr>
<tr>
<td></td>
<td>Atriplex falcata</td>
<td>30</td>
<td>0.021</td>
<td>6.9</td>
<td>1.608</td>
<td>0.925</td>
</tr>
<tr>
<td></td>
<td>Sitanion hystrix</td>
<td>30</td>
<td>0.060</td>
<td>25.9</td>
<td>3.544</td>
<td>0.744</td>
</tr>
<tr>
<td></td>
<td>Agropyron desertorum</td>
<td>30</td>
<td>0.062</td>
<td>30.1</td>
<td>15.456</td>
<td>0.731</td>
</tr>
<tr>
<td></td>
<td>Chrysothamnus viscidiflorus</td>
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<td>0.068</td>
<td>9.4</td>
<td>5.259</td>
<td>0.545</td>
</tr>
<tr>
<td></td>
<td>Chrysothamnus nauseosus</td>
<td>15</td>
<td>0.055</td>
<td>11.0</td>
<td>7.045</td>
<td>0.563</td>
</tr>
<tr>
<td></td>
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<td>0.010</td>
<td>1.0</td>
<td>0.745</td>
<td>0.444</td>
</tr>
<tr>
<td></td>
<td>Descurainia spp.</td>
<td>15</td>
<td>0.006</td>
<td>0.9</td>
<td>0.623</td>
<td>0.546</td>
</tr>
<tr>
<td></td>
<td>Lepidium perfoliatum</td>
<td>15</td>
<td>0.009</td>
<td>18.8</td>
<td>10.868</td>
<td>0.573</td>
</tr>
<tr>
<td></td>
<td>Bassia hyssopifolia</td>
<td>15</td>
<td>0.035</td>
<td>25.1</td>
<td>17.769</td>
<td>0.715</td>
</tr>
<tr>
<td>Fall</td>
<td>Sarcobatus vermiculatus</td>
<td>26</td>
<td>0.035</td>
<td>29.1</td>
<td>7.228</td>
<td>0.673</td>
</tr>
<tr>
<td></td>
<td>Atriplex confertilolia</td>
<td>64</td>
<td>0.036</td>
<td>9.7</td>
<td>7.228</td>
<td>0.673</td>
</tr>
<tr>
<td></td>
<td>Artemisia tridentata</td>
<td>41</td>
<td>0.035</td>
<td>21.5</td>
<td>12.170</td>
<td>0.846</td>
</tr>
<tr>
<td></td>
<td>Chrysothamnus viscidiflorus</td>
<td>26</td>
<td>0.029</td>
<td>14.5</td>
<td>5.332</td>
<td>0.843</td>
</tr>
<tr>
<td></td>
<td>Chrysothamnus nauseosus</td>
<td>26</td>
<td>0.040</td>
<td>17.2</td>
<td>9.589</td>
<td>0.602</td>
</tr>
<tr>
<td></td>
<td>Kochia americana</td>
<td>52</td>
<td>0.016</td>
<td>1.9</td>
<td>1.649</td>
<td>0.381</td>
</tr>
<tr>
<td></td>
<td>Atriplex falcata</td>
<td>24</td>
<td>0.058</td>
<td>19.3</td>
<td>4.795</td>
<td>0.831</td>
</tr>
<tr>
<td></td>
<td>Sitanion hystrix</td>
<td>39</td>
<td>0.016</td>
<td>3.3</td>
<td>2.119</td>
<td>0.642</td>
</tr>
<tr>
<td></td>
<td>Agropyron desertorum</td>
<td>29</td>
<td>0.036</td>
<td>10.1</td>
<td>5.277</td>
<td>0.719</td>
</tr>
<tr>
<td></td>
<td>Bromus tectorum</td>
<td>6</td>
<td>0.003</td>
<td>4.5</td>
<td>3.809</td>
<td>0.205</td>
</tr>
<tr>
<td></td>
<td>Sporobolus airoides</td>
<td>20</td>
<td>0.008</td>
<td>3.0</td>
<td>1.319</td>
<td>0.582</td>
</tr>
<tr>
<td></td>
<td>Halogeton glomeratus</td>
<td>30</td>
<td>0.016</td>
<td>30.1</td>
<td>32.172</td>
<td>0.465</td>
</tr>
<tr>
<td></td>
<td>Descurainia spp.</td>
<td>13</td>
<td>0.001</td>
<td>0.8</td>
<td>0.856</td>
<td>0.546</td>
</tr>
<tr>
<td></td>
<td>Lepidium perfoliatum</td>
<td>24</td>
<td>0.010</td>
<td>22.1</td>
<td>14.458</td>
<td>0.149</td>
</tr>
</tbody>
</table>
values in the same range as this study. Hutchings and Mason (1970) found the relationship to be generally more variable for shrubby species \((0.23 \leq r^2 \leq 0.87)\) than the present study. Westoby (1973) reported coefficients of determination for regressions of biomass with volume, for *Kochia americana* and *Chrysothamnus viscidiflorus*, of 0.71 and 0.76, respectively.

**Estimates of available herbage**

Available herbage (dry weight kg/ha), weighted by the proportions of jackrabbits taken at various locations, is summarized in Table 7. This weighting insures comparability to the stomach data which are also averages for the shooting area.

Species biomass is similar at all seasons to values reported for the US/IBP Curlew Valley Validation Site by Balph et al. (1974), Shinn et al. (1975) and MacMahon et al. (1976). Net primary production values as high as 2130 kg/ha were reported by MacMahon et al. (1976) for the *Artemisia-Atriplex-Sitanion* type in Curlew Valley.

There are no comparable data for *Atriplex falcata* because while it is abundant when found in pure stands, these stands do not occur over large areas in Curlew Valley. The calculated biomass values seem high, since *A. falcata* generally does not approach the biomass of *Atriplex confertifolia* and *Artemisia tridentata*. Its abundance in the shooting area is likely because jackrabbits were frequently collected in this open type.

The introduced forbs, *Halogeton* and *Bassia*, were abundant in all seasons although their forage quality was quite different in each
Table 7. Mean and standard error values for available dry biomass (kg/ha) along the shooting area for all rabbits shot away from crested wheat seedings in 1976 in Curlew Valley, Utah.

<table>
<thead>
<tr>
<th>Herbage type</th>
<th>Winter</th>
<th>Spring</th>
<th>Summer</th>
<th>Fall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sarcobatus vermiculatus</td>
<td>1193 ± 1002</td>
<td>936 ± 1131</td>
<td>1608 ± 510</td>
<td>1347 ± 1133</td>
</tr>
<tr>
<td>Atriplex confertifolia</td>
<td>1264 ± 566</td>
<td>1608 ± 1189</td>
<td>408 ± 145</td>
<td>76 ± 20</td>
</tr>
<tr>
<td>Artemisia tridentata</td>
<td>884 ± 370</td>
<td>170 ± 240</td>
<td>89 ± 90</td>
<td>67 ± 14</td>
</tr>
<tr>
<td>Chrysothamnus spp.</td>
<td>100 ± 57</td>
<td>132 ± 76</td>
<td>339 ± 39</td>
<td>135 ± 22</td>
</tr>
<tr>
<td>Kochia americana</td>
<td>76 ± 20</td>
<td>139 ± 97</td>
<td>13 ± 4</td>
<td>9 ± 13</td>
</tr>
<tr>
<td>Atriplex falcata</td>
<td>716 ± 106</td>
<td>131 ± 45</td>
<td>133 ± 17</td>
<td>10 ± 2</td>
</tr>
<tr>
<td>Sitanion hystrix</td>
<td>135 ± 22</td>
<td>72 ± 35</td>
<td>132 ± 103</td>
<td>13 ± 4</td>
</tr>
<tr>
<td>Bromus tectorum</td>
<td>72 ± 35</td>
<td>94 ± 71</td>
<td>133 ± 17</td>
<td>13 ± 4</td>
</tr>
<tr>
<td>Other grasses</td>
<td>7 ± 5</td>
<td>13 ± 4</td>
<td>2 ± 4</td>
<td>13 ± 4</td>
</tr>
<tr>
<td>Halogeton glomeratus</td>
<td>1344 ± 1494</td>
<td>678 ± 70</td>
<td>669 ± 89</td>
<td>1533 ± 1388</td>
</tr>
<tr>
<td>Bassia hyssopifolia</td>
<td>49 ± 22</td>
<td>541 ± 213</td>
<td>609 ± 473</td>
<td>113 ± 44</td>
</tr>
<tr>
<td>Descurainia spp.</td>
<td>18 ± 10</td>
<td>13 ± 10</td>
<td>28 ± 10</td>
<td>13 ± 10</td>
</tr>
<tr>
<td>Lepidium perfoliatum</td>
<td>27 ± 9</td>
<td>6 ± 9</td>
<td>6 ± 9</td>
<td>13 ± 10</td>
</tr>
<tr>
<td>Other forbs</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Totals</td>
<td>4497</td>
<td>5363</td>
<td>5121</td>
<td>5192</td>
</tr>
</tbody>
</table>
season. Together they provided in excess of 1200 kg/ha of available herbage.

The half-shrub, Kochia, was relatively abundant in Curlew Valley in 1976, compared to the estimates of Westoby (1973) in 1972. He estimated 2.3 kg/ha of Kochia as a yearly average availability, although he did observe one site with 23.6 kg/ha. Yearly average Kochia availability in the present study was 122 kg/ha. Jackrabbits were sampled in 1976 in habitats that may have had greater rooting density of Kochia than the sites that Westoby (1973) sampled. However, some of the samples in 1972 and 1976 came from nearly identical locations and available Kochia was greater in 1976 at these locations.

Note that for dominant shrubs such as Artemisia, Westoby (1973: 38) considered only young stems and leaves as "available." This accounts for the large difference in availability for these dominant species compared to the present study. New stems and leaves comprise about 10-15 percent of above ground biomass in these shrub species (Balph et al. 1974).

Dietary Composition and Preference

A total of 148 jackrabbits were collected for stomach analysis during 1976. Rabbits were taken throughout the study area (Figure 1); 61 were taken from within 0.5 km of the crested wheat seeding and 87 were taken further away.

Trial mixture results and calibrations

Table 8 shows the parameters of linear calibration regression equations derived from the analyses of mixtures of known composition.
Table 8. Parameters of calibration equations which are linear regressions of the form (Actual percentage) = a + b(Estimated percentage). Data are from analyses conducted by one observer on 33 mixtures of known composition. Cases where both actual and estimated percentages were zero were not included.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>n</th>
<th>Slope (b)</th>
<th>Mean actual percentage ($y_c$)</th>
<th>Standard error ($s_{y.x}$)</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Artemisia tridentata</td>
<td>15</td>
<td>1.197</td>
<td>21.693</td>
<td>16.681</td>
<td>0.626</td>
</tr>
<tr>
<td>Atriplex confertifolia</td>
<td>5</td>
<td>1.338</td>
<td>33.860</td>
<td>18.651</td>
<td>0.823</td>
</tr>
<tr>
<td>Sarcobatus vermiculatus</td>
<td>8</td>
<td>1.393</td>
<td>28.013</td>
<td>15.663</td>
<td>0.751</td>
</tr>
<tr>
<td>Chrysothamnus viscidiflorus</td>
<td>8</td>
<td>1.170</td>
<td>20.825</td>
<td>9.613</td>
<td>0.924</td>
</tr>
<tr>
<td>Kochia americana</td>
<td>15</td>
<td>0.683</td>
<td>16.347</td>
<td>11.039</td>
<td>0.644</td>
</tr>
<tr>
<td>Atriplex falcata</td>
<td>9</td>
<td>1.342</td>
<td>37.578</td>
<td>24.024</td>
<td>0.742</td>
</tr>
<tr>
<td>Sitanion hystrix</td>
<td>13</td>
<td>0.394</td>
<td>12.839</td>
<td>10.921</td>
<td>0.636</td>
</tr>
<tr>
<td>Agropyron desertorum</td>
<td>9</td>
<td>0.450</td>
<td>17.178</td>
<td>8.716</td>
<td>0.811</td>
</tr>
<tr>
<td>Bromus tectorum</td>
<td>11</td>
<td>2.001</td>
<td>9.900</td>
<td>11.020</td>
<td>0.227</td>
</tr>
<tr>
<td>Halogeton glomeratus</td>
<td>20</td>
<td>1.402</td>
<td>35.875</td>
<td>16.534</td>
<td>0.844</td>
</tr>
<tr>
<td>Bassia hyssopifolia</td>
<td>7</td>
<td>1.229</td>
<td>25.057</td>
<td>14.086</td>
<td>0.848</td>
</tr>
<tr>
<td>Salsola kali</td>
<td>6</td>
<td>0.806</td>
<td>6.017</td>
<td>4.706</td>
<td>0.606</td>
</tr>
<tr>
<td>Sphaeralcea munroana</td>
<td>4</td>
<td>1.445</td>
<td>4.800</td>
<td>1.256</td>
<td>0.971</td>
</tr>
</tbody>
</table>
These data reveal problems in applying the microscopic analysis techniques to browsers as do papers by Hansen and Flinders (1969) and Westoby et al. (1976). Grasses, most forbs, and other plants with easily identifiable epidermis were overestimated in the mixtures ($b < 1$). Woody species were underestimated ($b > 1$) because of the unidentifiability of woody fragments and because of overestimation of the easily identifiable components in the same mixture. Correlation coefficients of estimated percentage composition with the known percentage in the mixture ranged from 0.476 to 0.985, and were not appreciably improved by log transformation of the data. Ratios of the standard error of the estimate to the mean fraction of mixture item present ($\bar{y}_c/s_{y.x}$) ranged from roughly 0.5 to 1.0. The calibration parameters also indicate that there was a tendency to underestimate (or to miss entirely) species which were present in small amounts and to overestimate those present in large amounts. As a result of the interrelationship between the percentages of the components in any mixture, the calculation of corrected stomach content values from the calibration equations results in totals different from 100 percent.

Another method used to analyze the observer errors in the microscopic analysis was to calculate error rates for each species included in the trials. This error rate is the proportion of the mixtures in which a species occurred for which the observer failed to include, or included erroneously, that species. The average error rate for all species was 0.202, meaning a 20 percent error rate in identification. However, these mistakes were usually assignment to a species within the same forage type. For example, the error rates for Bromus
tectorum, Sitanion hystrix and Agropyron desertorum were 0.267, 0.278, and 0.400 respectively. The observer had no trouble (error rate less than 5 percent) determining that the fragments of the above were all grasses but might have made a mistake on the specific identification. One combination where assignment to the wrong species meant assignment to the wrong forage type was the two species of Atriplex, A. confertifolia (a dominant shrub) and A. falcata (a suffrutescent). The error rate of misidentification of A. falcata was low (0.100) but A. confertifolia was misidentified frequently (0.400). Most of the misidentifications of A. confertifolia occurred when it was found in mixtures that also contained A. falcata.

The following conclusions about the microscopic analysis were drawn:

(1) The microscopic analysis procedure of Sparks and Malechek (1968) has limitations when applied to browsers.

(2) There is a tendency to overestimate material that is mostly epidermis (grass and forbs) and/or present in large amounts.

(3) There is a tendency to underestimate material that is mostly woody and/or present in small amounts.

(4) Calibration equations are largely useless in deriving corrected estimates but are useful analyses of observer bias.

These conclusions are similar to those of Westoby et al. (1976) who also applied the technique to jackrabbits. Observer biases were similar, as were the rates of misidentification and the occurrence of unknowns. Hereafter, all dietary percentages reported are
uncorrected values and comparisons with other data employ only the uncorrected percentages.

**Summary of dietary composition**

Means and variances of stomach contents for all samples in each season are given in Appendix D and all plant taxa occurring in the plant samples are separated as far as possible in the dietary analysis. Months were combined into seasons as follows: winter (December-February), spring (March-May), summer (June-August), and fall (September-November). The data in Table 9 have been lumped into broader types of forage: dominant shrubs which include, primarily, *Artemisia tridentata*, *Sarcobatus vermiculatus* and *Atriplex confertifolia*; suffrutescents which are *Kochia americana* and *Atriplex falcata*; *Chrysothamnus* spp. which includes both *C. viscidiflorus* and *C. nauseosus*; grasses which include *Sitanion hystrix*, *Agropyron desertorum* and *Bromus tectorum* and forbs other than *Halogeton* which includes, primarily, *Bassia hyssopifolia*, *Lepidium perfoliatum*, *Descurainia* spp., *Salsola kali* and *Sphaeralcea munroana*.

The general features of the jackrabbits' diet are summarized as follows:

1. Dominant shrubs are the main forage taken in fall and winter.
2. Grasses are important in spring and summer.
3. Forbs, other than *Halogeton*, are a major component in summer.
4. *Halogeton* is never a highly predominant component in any season.
Table 9. Mean percentage separated by season of forage types in stomach contents of all jackrabbits shot in Curlew Valley, Utah during 1976, and Kruskal-Wallis statistics (H) from the analyses of seasonal variation.

<table>
<thead>
<tr>
<th>Forage type</th>
<th>Percentage of total stomach contents</th>
<th></th>
<th></th>
<th></th>
<th></th>
<th>H^a</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Winter</td>
<td>Spring</td>
<td>Summer</td>
<td>Fall</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dominant shrubs</td>
<td>64.68</td>
<td>14.91</td>
<td>3.52</td>
<td>34.61</td>
<td></td>
<td>57.29^b</td>
</tr>
<tr>
<td>Suffrutescent</td>
<td>15.79</td>
<td>5.91</td>
<td>2.22</td>
<td>22.43</td>
<td></td>
<td>19.48^b</td>
</tr>
<tr>
<td>Chrysothamnus spp.</td>
<td>1.71</td>
<td>0.20</td>
<td>8.98</td>
<td>4.90</td>
<td></td>
<td>33.79^b</td>
</tr>
<tr>
<td>Grasses (including A. desertorum)</td>
<td>0.22</td>
<td>51.27</td>
<td>47.83</td>
<td>19.26</td>
<td></td>
<td>52.09^b</td>
</tr>
<tr>
<td>Halogeton sp.</td>
<td>7.89</td>
<td>12.78</td>
<td>3.71</td>
<td>6.26</td>
<td></td>
<td>8.90^c</td>
</tr>
<tr>
<td>Forbs</td>
<td>6.35</td>
<td>9.89</td>
<td>30.39</td>
<td>9.28</td>
<td></td>
<td>44.47^b</td>
</tr>
<tr>
<td>Unknowns</td>
<td>3.36</td>
<td>5.24</td>
<td>3.35</td>
<td>3.26</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of stomachs</td>
<td>16</td>
<td>48</td>
<td>45</td>
<td>39</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

^a 3 degrees of freedom in each case.

^b p ≤ .001.

^c p ≤ .05.
(5) Suffrutescents (Kochia, Atriplex falcata) were variable and sometimes (fall and winter) important components.

Studies conducted throughout the black-tailed jackrabbits' range have shown that grasses are important food items during early spring and summer, forbs during the summer, and shrubs in fall and winter (Currie and Goodwin 1966, Hayden 1966, Sparks 1968, Flinders and Hansen 1972, Uresk 1978). Only Westoby (1973) emphasized the importance of suffrutescents and Halogeton in jackrabbit diets. In his studies, Kochia was important in spring and fall and Halogeton was important in all seasons, especially fall and winter.

These seasonal patterns were examined for each forage type using a Kruskal-Wallis statistic (Sokal and Rohlf 1969: 388-389) (Table 9). For each forage type there is a significant ($p \leq 0.05$) or highly significant ($p \leq 0.001$) shift in the importance between seasons.

The data from the "natural" habitats, away from the crested wheatgrass seedings, are treated separately, because I wanted to compare the results directly to Westoby (1973) who excluded habitats in the vicinity of crested wheat. The patterns (Table 10) are similar to samples including both areas. As might be expected, there is a decrease in the importance of grasses in the diet, and an increase in the importance of shrubs. Using a Wilcoxon two sample test (Sokal and Rohlf 1969:383) the percentages of grass in stomachs of jackrabbits shot near the seedings were compared (Table 11) with those shot away from the seedings, for all seasons for which there were data. The stomachs of jackrabbits shot near the seedings contained
Table 10. Mean percentage separated by seasons of forage classes in stomach contents of jackrabbits shot far from the crested wheatgrass seedings in Curlew Valley, Utah during 1976.

<table>
<thead>
<tr>
<th>Forage type</th>
<th>Percentage of stomach contents</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Winter</td>
<td>Spring</td>
<td>Summer</td>
<td>Fall</td>
</tr>
<tr>
<td>Dominant shrubs</td>
<td>64.68</td>
<td>14.31</td>
<td>5.73</td>
<td>53.73</td>
</tr>
<tr>
<td>Suffrutescents</td>
<td>15.79</td>
<td>5.54</td>
<td>2.66</td>
<td>28.96</td>
</tr>
<tr>
<td>Chrysothamnus spp.</td>
<td>1.71</td>
<td>0.70</td>
<td>13.98</td>
<td>0.42</td>
</tr>
<tr>
<td>Grasses</td>
<td>0.22</td>
<td>45.72</td>
<td>30.73</td>
<td>3.17</td>
</tr>
<tr>
<td>Halogeton sp.</td>
<td>7.89</td>
<td>16.21</td>
<td>4.64</td>
<td>5.93</td>
</tr>
<tr>
<td>Forbs</td>
<td>6.35</td>
<td>11.63</td>
<td>43.21</td>
<td>3.30</td>
</tr>
<tr>
<td>Unknowns</td>
<td>3.36</td>
<td>5.89</td>
<td>0.00</td>
<td>4.49</td>
</tr>
<tr>
<td>Number of stomachs</td>
<td>16</td>
<td>31</td>
<td>22</td>
<td>18</td>
</tr>
</tbody>
</table>
significantly more grass than those shot away from the seedings \( (t_s = 9.88, p \leq 0.001) \).

Table 11. Comparison of mean percentage of grasses, separated by seasons, in the stomach contents of jackrabbits shot within 0.5 km of the crested wheatgrass seeding with those shot away from the seeding, during 1976 in Curlew Valley, Utah.

<table>
<thead>
<tr>
<th>Sample location</th>
<th>Sample size</th>
<th>Winter</th>
<th>Spring</th>
<th>Summer</th>
<th>Fall</th>
</tr>
</thead>
<tbody>
<tr>
<td>Away from seeding</td>
<td>71</td>
<td>0.22</td>
<td>45.72</td>
<td>30.73</td>
<td>3.17</td>
</tr>
<tr>
<td>Near seeding</td>
<td>61</td>
<td>-</td>
<td>61.39</td>
<td>64.19</td>
<td>33.05</td>
</tr>
</tbody>
</table>

Preference values

Using the dietary composition data and herbage availability data, dietary preference values (Petrides 1975) can be calculated. The preference rating was calculated by dividing the dietary percentage by the relative availability (Table 7) in the habitat. Biomass may be different for two areas, but the relative proportions from which the animal is selecting may be the same. However, the preference ratings are regarded as a guide to food preferences rather than absolute values because of the difficulty in measuring availability.

Table 12 presents preference ratings for each of the four seasons for jackrabbits shot far from the wheatgrass seedings. Although
Table 12. Dietary preference ratings for rabbits shot far from the crested wheatgrass seedings during 1976 in Curlew Valley, Utah.

<table>
<thead>
<tr>
<th>Forage type</th>
<th>Winter (n = 16)</th>
<th>Spring (n = 31)</th>
<th>Summer (n = 22)</th>
<th>Fall (n = 18)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Relative availability (a)</td>
<td>Dietary proportion (d)</td>
<td>Preference rating p = d/a</td>
<td></td>
</tr>
<tr>
<td>Dominant shrubs</td>
<td>46.19</td>
<td>64.68</td>
<td>1.40</td>
<td></td>
</tr>
<tr>
<td>Suffrutescents</td>
<td>17.61</td>
<td>15.79</td>
<td>0.90</td>
<td></td>
</tr>
<tr>
<td>Chrysothamnus spp.</td>
<td>2.22</td>
<td>1.71</td>
<td>0.77</td>
<td></td>
</tr>
<tr>
<td>Grasses</td>
<td>3.00</td>
<td>0.22</td>
<td>0.07</td>
<td></td>
</tr>
<tr>
<td>Halogeton sp.</td>
<td>29.89</td>
<td>7.89</td>
<td>0.26</td>
<td></td>
</tr>
<tr>
<td>Forbs</td>
<td>1.09</td>
<td>6.35</td>
<td>5.83</td>
<td></td>
</tr>
<tr>
<td></td>
<td>62.84</td>
<td>14.31</td>
<td>0.23</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6.41</td>
<td>5.54</td>
<td>0.86</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2.46</td>
<td>0.70</td>
<td>0.28</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4.72</td>
<td>45.72</td>
<td>9.69</td>
<td></td>
</tr>
<tr>
<td></td>
<td>12.64</td>
<td>16.21</td>
<td>1.28</td>
<td></td>
</tr>
<tr>
<td></td>
<td>10.93</td>
<td>11.63</td>
<td>1.06</td>
<td></td>
</tr>
<tr>
<td></td>
<td>58.24</td>
<td>5.73</td>
<td>0.10</td>
<td></td>
</tr>
<tr>
<td></td>
<td>5.27</td>
<td>2.66</td>
<td>0.50</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6.62</td>
<td>13.98</td>
<td>2.11</td>
<td></td>
</tr>
<tr>
<td></td>
<td>4.55</td>
<td>30.73</td>
<td>6.75</td>
<td></td>
</tr>
<tr>
<td></td>
<td>13.06</td>
<td>4.64</td>
<td>0.36</td>
<td></td>
</tr>
<tr>
<td></td>
<td>12.26</td>
<td>43.21</td>
<td>3.52</td>
<td></td>
</tr>
<tr>
<td></td>
<td>51.39</td>
<td>53.73</td>
<td>1.05</td>
<td></td>
</tr>
<tr>
<td></td>
<td>11.88</td>
<td>28.96</td>
<td>2.44</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1.71</td>
<td>0.42</td>
<td>0.25</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2.77</td>
<td>3.17</td>
<td>1.14</td>
<td></td>
</tr>
<tr>
<td></td>
<td>29.53</td>
<td>5.93</td>
<td>0.20</td>
<td></td>
</tr>
<tr>
<td></td>
<td>2.72</td>
<td>3.30</td>
<td>1.21</td>
<td></td>
</tr>
</tbody>
</table>
jackrabbits eat nearly any herbage that occurs on the study area, preference ratings show that they do not simply feed in proportion to availability. Preference ratings confirm patterns drawn from the composition data alone. Dominant shrubs have preference ratings greater than one in winter and fall. Grasses have high preference ratings in spring and summer. Forbs have preference ratings greater than one in all seasons. On the basis of these calculations, *Halgate* was preferred only in spring and suffrutescents only in fall.

Uresk (1978) calculated preference ratings based on the relative occurrence of plants in fecal pellets for sagebrush habitats in Washington. The most common grass (*Stipa comata*) had a preference rating of 110. *Artemisia tridentata* had an average preference of 0.5 and *Chrysothamnus nauseosus* had an average preference rating of 70. These high preference ratings for the grass and *Chrysothamnus* are different from the present study, while the value for *Artemisia* is similar. The wide discrepancy of the values emphasizes the difficulty in attaching significance to the absolute value of preference ratings.

**Comparisons of diets during high and low density periods**

Using the data presented by Westoby (1973:64) and the dietary data of the present study, statistical comparisons were made between the diets in periods of high and low density. Two kinds of data were used for the tests; (1) the dietary proportions and (2) preference ratings. Variability could not be estimated from the data of Westoby (1973), but non-parametric tests of location were made (Friedman's statistic \(X^2\), Sokal and Rohlf 1969:398) along with
analyses of variance assuming similar error. Each forage type was treated separately, and seasons were treated as blocks since their effect has already been established (Table 9). None of the dietary components occurred in significantly different proportions for the two density periods based on the Friedman's statistics (Table 13).

Unweighted mean dietary proportions were subjected to analyses of variance ignoring distributional difficulties with the percentage data. These tests (Table 13) show no significant differences between periods for any forage type. These analyses are presented in support of the non-parametric tests. The analysis of variance is generally the more efficient statistical test even when the assumptions hold only approximately (Sokal and Rohlf 1969).

The above tests on dietary proportions assume that diet selection during the two periods was not constrained by availability. The analyses ignore complications that are introduced by the differences in measurements of herbage availability. These results constitute the failure to reject a form of hypothesis $H(3)$, that average dietary composition was not significantly different in high (1971-1972) and low (1976) density periods.

Preference ratings from the two periods (Table 14) were also compared using the Friedman's statistic. Based on the ranks of the five groups for which there is data from both periods, average preferences are not significantly different ($X^2 = 1.80, p > 0.05$). Note that this comparison is based on ranking preferences for each forage type and is not influenced by the value of the preference rating. The high preferences calculated from Westoby's data for
Table 13. Comparison of dietary composition of individual forage types for jackrabbits taken far from the crested wheatgrass seeding in years of high population density (1971-1972, Westoby 1973) and a year of low population density (1976, present study).

<table>
<thead>
<tr>
<th>Forage type</th>
<th>$X^2^a$</th>
<th>$F^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant shrubs</td>
<td>0.00$^C$</td>
<td>1.90$^C$</td>
</tr>
<tr>
<td>Suffrutescents</td>
<td>0.00$^C$</td>
<td>0.48$^C$</td>
</tr>
<tr>
<td>Chrysothamnus spp.</td>
<td>0.00$^C$</td>
<td>0.26$^C$</td>
</tr>
<tr>
<td>Grasses</td>
<td>1.00$^C$</td>
<td>0.12$^C$</td>
</tr>
<tr>
<td>Halogeton sp.</td>
<td>2.25$^C$</td>
<td>5.58$^d$</td>
</tr>
<tr>
<td>Forbs</td>
<td>1.00$^C$</td>
<td>2.48$^C$</td>
</tr>
</tbody>
</table>

---

$a$ Friedman's statistic, degrees of freedom equals 1 in all cases.

$b$ Analyses of variance, degrees of freedom for F statistics 1 and 3 in all cases.

$c$ Not significant, $p > 0.05$.

$d$ $0.01 > p > 0.05$. 
Table 14. Average dietary preference values of individual forage types of jackrabbits taken in a year of high population density (1972, Westoby 1973) and a year of low population density (1976, present study).

<table>
<thead>
<tr>
<th>Forage type</th>
<th>Preference rating</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Westoby(^a)</td>
<td>This study</td>
<td></td>
</tr>
<tr>
<td>Dominant shrubs</td>
<td>0.39</td>
<td>0.70</td>
<td></td>
</tr>
<tr>
<td>Suffrutescents</td>
<td>36.00(^b)</td>
<td>1.18</td>
<td></td>
</tr>
<tr>
<td>Chrysothamnus spp.</td>
<td>1.75</td>
<td>0.85</td>
<td></td>
</tr>
<tr>
<td>Grasses</td>
<td>52.50</td>
<td>4.41</td>
<td></td>
</tr>
<tr>
<td>Halogeton sp.</td>
<td>0.69</td>
<td>0.53</td>
<td></td>
</tr>
<tr>
<td>Forbs</td>
<td>-</td>
<td>2.91</td>
<td></td>
</tr>
</tbody>
</table>

\(^a\) Data from Table 12 (Westoby 1973:64).

\(^b\) Based only on reported values for Kochia.
suffrutescents and grasses are undoubtedly due to differences in estimated availability. These results fail to reject another form of hypothesis H(3). Jackrabbit preferences were not different with respect to available herbage in either period of the population cycle. Flinders and Hansen (1972) used mean preference values in a similar fashion to compare diet selection of Colorado jackrabbits. They contend that preference values "indicate the relative amounts of energy expended by these hares in searching for the foods in their diets" (Flinders and Hansen 1972:25) and that they therefore reflect differences of ecological importance.

Comparisons of diets between sexes

Comparisons similar to those above were made between adult males and females during the breeding season (January-May) in 1976. The percentage occurrence of each forage type in stomachs of 21 females and 26 males was compared using Kruskal-Wallis statistics (Table 15). The test failed to reject the hypothesis H(4), that diet composition was not different between sexes during the breeding season.

Statistics comparing preference ratings between sexes during the breeding season are presented in Table 15. This test failed to reject H(4). Flinders and Hansen (1972) found no significant differences between preference indexes of male and female black-tailed and white-tailed jackrabbits.
Table 15. Kruskal-Wallis statistics (H) from the analyses of proportion and preference ratings for individual forage types between sexes (adult female and adult male) of jackrabbits collected during the breeding season (January through May) in 1976 in Curlew Valley, Utah. All samples were from jackrabbits taken away from crested wheatgrass seedings. The degrees of freedom is 1 in all cases.

<table>
<thead>
<tr>
<th>Forage type</th>
<th>Diet proportion</th>
<th>Preference rating</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dominant shrubs</td>
<td>0.28&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.21&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Suffrutescents</td>
<td>0.50&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.83&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Chrysothamnus spp.</td>
<td>1.34&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.34&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Grasses</td>
<td>0.18&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.02&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Halogeton sp.</td>
<td>0.01&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.01&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Forbs</td>
<td>0.66&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.25&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

<sup>a</sup> Not significant, p > 0.05.
Analysis of Composition Versus Availability

Intensive plant sampling in the vicinity of each jackrabbit collection site allowed diet composition to be related directly to availability. The data were used to test the prediction that the percentage that a forage type composed of a diet should be unrelated to availability above about 10 kg/ha (Westoby 1974). If this were the case, the contribution of a forage type to the diet should not change over a wide range of availability. To test this hypothesis the slope of a regression of percent in diet against available biomass is compared with zero.

Data from jackrabbits taken near the crested wheatgrass seeding were used in the analysis because: (1) collection locations were most accurately determined for these samples, and (2) because these vegetation samples showed a wide range of available herbage. Figures 10 through 14 are scatter plots of the percent of a forage type in the diet as a function of the available dry biomass (kg/ha) of that forage type. Results of the regression analysis are shown in Table 16. *Atriplex confertifolia* had a slope constant (b) significantly different from zero, but negative. This is not predicted by the Westoby hypothesis H(1). *Halogeton* had a slope (b) with a negative sign, but it was not statistically different from zero. The other three forage types tested, *Atriplex falcata*, grasses, and *Bassia*, had slopes significantly greater than zero. Note that the
Figure 10. Percent of the individual's diet composed of *Atriplex confertifolia* (dominant shrub), as a function of availability.
Figure 11. Percent of the individual's diet composed of *Atriplex falcata* (suffrutescent), as a function of availability.
Figure 12. Percent of the individual's diet composed of grasses, as a function of availability.
Figure 13. Percent of the individual's diet composed of *Halogeton glomeratus* (forb), as a function of availability.
Figure 14. Percent of the individual’s diet composed of *Bassia hyssopifolia* (forb) as a function of availability.
Table 16. Results of linear regression analyses of percent of diet with available biomass (kg/ha) of selected forage types during 1976 in Curlew Valley, Utah. Significance level is for the test of Ho: \( b = 0 \).

<table>
<thead>
<tr>
<th>Forage type</th>
<th>n</th>
<th>b</th>
<th>r²</th>
<th>F</th>
<th>Significance level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atriplex confertifolia</td>
<td>42</td>
<td>-0.009</td>
<td>0.100</td>
<td>4.451</td>
<td>( p &lt; 0.05 )</td>
</tr>
<tr>
<td>Atriplex falcata</td>
<td>30</td>
<td>0.081</td>
<td>0.504</td>
<td>28.431</td>
<td>( p &lt; 0.001 )</td>
</tr>
<tr>
<td>Grasses</td>
<td>44</td>
<td>0.033</td>
<td>0.205</td>
<td>10.855</td>
<td>( p &lt; 0.005 )</td>
</tr>
<tr>
<td>Halogeton glomeratus</td>
<td>46</td>
<td>-0.001</td>
<td>0.004</td>
<td>0.161</td>
<td>NS(^a)</td>
</tr>
<tr>
<td>Bassia hyssopifolia</td>
<td>34</td>
<td>0.044</td>
<td>0.416</td>
<td>22.784</td>
<td>( p &lt; 0.001 )</td>
</tr>
</tbody>
</table>

\(^a\) NS signifies \( p > 0.05 \).
lower limit of availabilities for these relationships approached the limit of 10 kg/ha which was suggested by Westoby (1974) as the point below which dietary occurrence should fall to zero. Since available biomass included values in the upper range for salt desert types (Balph et al. 1974), hypothesis H(1), that dietary composition will not be affected by changes in availability, can be rejected. In fact, some correlations are surprisingly good considering the difficulty in measuring the variables involved. For example, 50 percent of the variability of occurrence of Atriplex falcata in jackrabbit diets can be explained by differences in availability in the feeding habitat.

Herbage Utilization

The herbage utilization was measured on the two livestock proof exclosures from June 1976 to February 1978. During the first two sampling periods, no estimate of density, or total standing crop biomass, was obtained. Utilization is herein defined as removal, that is, consumption plus wastage.

Ocular estimates and calibration equations

Biomass per plant was estimated to facilitate utilization estimates and to give data on total removal. The regression parameters of the biomass calibration trials are given in Table 17. The coefficients of determination \( r^2 \) ranged from 0.704 to 0.965, which are similar to values given by Tadmor et al. (1975). Sitanion was consistently estimated less precisely than Kochia, probably
Table 17. Parameters of biomass calibration equations which are linear regressions of the form (Actual biomass) = a + b(Estimated biomass).

<table>
<thead>
<tr>
<th>Sampling date</th>
<th>Species</th>
<th>Observer</th>
<th>n</th>
<th>Slope (b)</th>
<th>Mean actual biomass ((\bar{y}_c))</th>
<th>Standard error ((s_{y-x}))</th>
<th>r^2</th>
</tr>
</thead>
<tbody>
<tr>
<td>June 1976</td>
<td>Kochia sp.</td>
<td>1</td>
<td>38</td>
<td>1.122</td>
<td>31.1</td>
<td>11.066</td>
<td>0.704</td>
</tr>
<tr>
<td></td>
<td>Kochia sp.</td>
<td>2</td>
<td>18</td>
<td>1.012</td>
<td>28.4</td>
<td>8.340</td>
<td>0.872</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>1</td>
<td>48</td>
<td>0.810</td>
<td>16.3</td>
<td>3.594</td>
<td>0.829</td>
</tr>
<tr>
<td>September 1976</td>
<td>Kochia sp.</td>
<td>1</td>
<td>50</td>
<td>1.113</td>
<td>22.1</td>
<td>3.684</td>
<td>0.950</td>
</tr>
<tr>
<td></td>
<td>Kochia sp.</td>
<td>2</td>
<td>50</td>
<td>1.201</td>
<td>24.8</td>
<td>6.347</td>
<td>0.909</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>1</td>
<td>50</td>
<td>0.699</td>
<td>5.9</td>
<td>2.015</td>
<td>0.770</td>
</tr>
<tr>
<td>February 1977</td>
<td>Kochia sp.</td>
<td>1</td>
<td>50</td>
<td>1.147</td>
<td>24.9</td>
<td>3.144</td>
<td>0.965</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>1</td>
<td>50</td>
<td>0.811</td>
<td>6.3</td>
<td>1.940</td>
<td>0.874</td>
</tr>
<tr>
<td>June 1977</td>
<td>Kochia sp.</td>
<td>1</td>
<td>50</td>
<td>1.107</td>
<td>23.9</td>
<td>3.722</td>
<td>0.955</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>1</td>
<td>50</td>
<td>1.048</td>
<td>9.7</td>
<td>2.487</td>
<td>0.887</td>
</tr>
<tr>
<td>September 1977</td>
<td>Kochia sp.</td>
<td>1</td>
<td>50</td>
<td>1.094</td>
<td>24.7</td>
<td>4.988</td>
<td>0.930</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>1</td>
<td>50</td>
<td>1.095</td>
<td>10.1</td>
<td>2.786</td>
<td>0.853</td>
</tr>
<tr>
<td>February 1978</td>
<td>Kochia sp.</td>
<td>1</td>
<td>50</td>
<td>0.895</td>
<td>11.0</td>
<td>2.607</td>
<td>0.913</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>1</td>
<td>50</td>
<td>0.867</td>
<td>7.0</td>
<td>1.662</td>
<td>0.773</td>
</tr>
</tbody>
</table>
because Sitanion plants had smaller mean weight and minor error in estimated weight was often a substantial proportion of the plant weight. Observers seem to learn since coefficients of determination were higher after the first sample.

Calibrations of utilization per plant were done like the ocular estimates of biomass (Table 18), but sample sizes in the first sampling period were inadequate. More experience was needed before observers reached satisfactory levels of precision in estimating utilization. Coefficients of determination ranged from 0.008 to 0.938 and neither species was consistently estimated more precisely.

In most cases, estimated mean removal per plant was higher in the calibration trials than in the samples because; (1) an attempt was made to simulate a wide range of removal intensity, and (2) actual removal per plant was lower than anticipated. Difference in estimated values between calibration and samples increases the variance of the estimate (Tadmor et al. 1975).

Summary of biomass and utilization

Table 19 gives the calibrated estimates of mean biomass and utilization per plant for 1976 to 1978. No calibration equations were calculated for Sitanion utilization in the first sampling period so the means for removal are uncalibrated values. Kochia plants were considerably larger in the north than in the south exclosure. Sitanion plants had about the same biomass in the two locations, but were less abundant in the south exclosure. Standing crop biomass of individual Kochia plants in the north exclosure declined throughout the study.
Table 18. Parameters of utilization calibration equations which are linear regressions of the form \((\text{Actual percentage removal}) = a + b(\text{Estimated percentage removal})\). Cases where both actual and estimated removal were zero were not included in the calibrations.

<table>
<thead>
<tr>
<th>Sampling date</th>
<th>Species</th>
<th>Observer</th>
<th>n</th>
<th>Slope (b)</th>
<th>Mean actual percent removal (\bar{y}_c)</th>
<th>Standard error (s_{\bar{y},x})</th>
<th>(r^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>June 1976</td>
<td>Kochia sp. 1</td>
<td>1</td>
<td>12</td>
<td>0.133</td>
<td>18.3</td>
<td>6.682</td>
<td>0.008</td>
</tr>
<tr>
<td></td>
<td>Kochia sp. 2</td>
<td>2</td>
<td>12</td>
<td>0.547</td>
<td>14.1</td>
<td>4.655</td>
<td>0.496</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td></td>
<td></td>
<td>no data</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>September 1976</td>
<td>Kochia sp. 1</td>
<td>1</td>
<td>50</td>
<td>0.797</td>
<td>41.5</td>
<td>8.561</td>
<td>0.647</td>
</tr>
<tr>
<td></td>
<td>Kochia sp. 2</td>
<td>2</td>
<td>50</td>
<td>0.918</td>
<td>41.8</td>
<td>10.112</td>
<td>0.672</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>1</td>
<td>50</td>
<td>0.730</td>
<td>40.1</td>
<td>11.656</td>
<td>0.490</td>
</tr>
<tr>
<td>February 1977</td>
<td>Kochia sp. 1</td>
<td>1</td>
<td>50</td>
<td>1.162</td>
<td>41.7</td>
<td>6.069</td>
<td>0.909</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>1</td>
<td>50</td>
<td>1.167</td>
<td>48.1</td>
<td>5.963</td>
<td>0.938</td>
</tr>
<tr>
<td>June 1977</td>
<td>Kochia sp. 1</td>
<td>1</td>
<td>50</td>
<td>0.865</td>
<td>41.0</td>
<td>5.625</td>
<td>0.843</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>1</td>
<td>50</td>
<td>1.015</td>
<td>44.9</td>
<td>5.469</td>
<td>0.938</td>
</tr>
<tr>
<td>September 1977</td>
<td>Kochia sp. 1</td>
<td>1</td>
<td>50</td>
<td>1.075</td>
<td>38.5</td>
<td>5.973</td>
<td>0.923</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>1</td>
<td>50</td>
<td>0.991</td>
<td>40.2</td>
<td>5.817</td>
<td>0.928</td>
</tr>
<tr>
<td>February 1978</td>
<td>Kochia sp. 1</td>
<td>1</td>
<td>50</td>
<td>0.773</td>
<td>47.0</td>
<td>6.996</td>
<td>0.855</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>1</td>
<td>50</td>
<td>0.823</td>
<td>46.7</td>
<td>6.781</td>
<td>0.846</td>
</tr>
</tbody>
</table>
Table 19. Calibrated estimates of mean biomass (g/plant) and utilization (percentage removal/plant) of two species of forage plants sampled in livestock-proof exclosures during 1976 to 1978 in Curlew Valley, Utah. Means given with standard errors. Sample size is in parentheses.

<table>
<thead>
<tr>
<th>Sampling date</th>
<th>Species</th>
<th>Biomass</th>
<th>Percentage removal per plant</th>
<th>Percentage of plants browsed</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>North</td>
<td>South</td>
<td>North</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June 1976</td>
<td>Kochia sp.</td>
<td>23.9 ± 1.9 (481)</td>
<td>1.5 ± 2.0 (560)</td>
<td>10.9 ± 2.0 (6)</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>13.3 ± 1.1 (354)</td>
<td>13.4 ± 1.1 (136)</td>
<td>10.0a</td>
</tr>
<tr>
<td>September 1976</td>
<td>Kochia sp.</td>
<td>20.1 ± 1.8 (380)</td>
<td>2.3 ± 1.2 (931)</td>
<td>31.0 ± 3.3 (29)</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>6.7 ± 0.6 (274)</td>
<td>6.0 ± 0.6 (140)</td>
<td>29.6 ± 3.0 (10)</td>
</tr>
<tr>
<td>February 1977</td>
<td>Kochia sp.</td>
<td>13.4 ± 1.0 (354)</td>
<td>1.2 ± 1.4 (296)</td>
<td>64.9 ± 9.3 (49)</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>6.0 ± 0.5 (163)</td>
<td>5.9 ± 0.6 (140)</td>
<td>48.0 ± 7.6 (3)</td>
</tr>
<tr>
<td>June 1977</td>
<td>Kochia sp.</td>
<td>9.9 ± 0.9 (301)</td>
<td>2.5 ± 0.8 (275)</td>
<td>13.2 ± 1.9 (2)</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>2.7 ± 0.6 (176)</td>
<td>5.2 ± 0.6 (141)</td>
<td>30.0 ± 6.6 (4)</td>
</tr>
<tr>
<td>September 1977</td>
<td>Kochia sp.</td>
<td>8.4 ± 1.1 (311)</td>
<td>1.6 ± 1.3 (239)</td>
<td>42.2 ± 4.3 (13)</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>6.4 ± 0.6 (186)</td>
<td>5.7 ± 0.7 (131)</td>
<td>18.2 ± 1.4 (3)</td>
</tr>
<tr>
<td>February 1978</td>
<td>Kochia sp.</td>
<td>5.8 ± 0.5 (272)</td>
<td>3.3 ± 0.5 (212)</td>
<td>45.9 ± 1.9 (105)</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>3.9 ± 0.4 (144)</td>
<td>3.5 ± 0.4 (121)</td>
<td>41.7 ± 1.7 (2)</td>
</tr>
<tr>
<td>Unweighted means</td>
<td>Kochia sp.</td>
<td>13.6</td>
<td>2.1</td>
<td>34.7</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>6.5</td>
<td>6.6</td>
<td>29.6</td>
</tr>
</tbody>
</table>

a Uncalibrated estimates.
No explanation is offered for the decline except that it was very dry during the growing season, September 1976 to August 1977, in which only 220 mm of precipitation (at Snowville, Utah, 25 km from the site) were received. Such climatic patterns are known to effect shoot growth and litter processes of similar suffrutescents like *Ceratoides lanata* (West and Fareed 1973). Standing crop patterns were more erratic in the south exclosure, with larger associated standard errors.

Biomass for *Sitanion* includes all above ground material. September and February measures are of standing crop of dried grass, while the June measure is of both dry and fresh material. There is a wide variation in moisture and nutritional properties, but jack-rabbits take grasses under both conditions.

Removal per plant was generally greater for *Kochia* than for *Sitanion* (Table 19) but this relationship varied seasonally. Browsed plants lost 20-40 percent, but the percentage of plants browsed was low; 38.6 percent of the plants were browsed in February 1978 but that was unusually high. Less than 10 percent of the *Kochia* plants were browsed in 75 percent of the sampling periods. Less than 10 percent of the *Sitanion* plants were ever browsed.

**Seasonal and Exclosure Comparisons**

Analysis of variance of the unweighted mean biomass per plant (Table 20) shows that *Kochia* biomass was significantly different among exclosures, years and seasons, and two-way interactions of these
Table 20. Analyses of variance of unweighted mean biomass per plant on plots sampled in livestock proof exclosures during 1976 to 1978 in Curlew Valley, Utah.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Kochia MS</th>
<th>F</th>
<th>Significance</th>
<th>Kochia F</th>
<th>Significance</th>
<th>Silticon MS</th>
<th>Silticon F</th>
<th>Significance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>287</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exclusion</td>
<td>1</td>
<td>6361.03</td>
<td>51.78</td>
<td>p ≤ .001</td>
<td>80.10</td>
<td>2.14</td>
<td>NS</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Plots (Excl.)</td>
<td>46</td>
<td>122.85</td>
<td></td>
<td></td>
<td>37.37</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>5026.61</td>
<td>273.95</td>
<td>p ≤ .001</td>
<td>2459.35</td>
<td>435.32</td>
<td>p ≤ .001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Season</td>
<td>2</td>
<td>724.06</td>
<td>39.46</td>
<td>p ≤ .001</td>
<td>278.35</td>
<td>38.65</td>
<td>p ≤ .001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year x Seas.</td>
<td>2</td>
<td>175.62</td>
<td>9.57</td>
<td>p ≤ .001</td>
<td>290.38</td>
<td>51.40</td>
<td>p ≤ .001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Excl. x Year</td>
<td>1</td>
<td>1558.15</td>
<td>84.92</td>
<td>p ≤ .001</td>
<td>25.25</td>
<td>4.47</td>
<td>p ≤ .001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Excl. x Seas.</td>
<td>2</td>
<td>160.59</td>
<td>8.75</td>
<td>p ≤ .001</td>
<td>26.11</td>
<td>4.62</td>
<td>p ≤ .05</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Excl. x Year x Seas.</td>
<td>2</td>
<td>11.05</td>
<td>0.60</td>
<td>NS</td>
<td>15.96</td>
<td>2.82</td>
<td>p ≤ .05</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>230</td>
<td>18.35</td>
<td></td>
<td></td>
<td>5.65</td>
<td></td>
<td>NS</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*NS signifies p > .05.
factors were significant. Sitanion biomass was not different between exclosures but yearly and seasonal variation was significant.

Results of analysis of variance of the utilization (Table 21) of Kochia show the three-way interaction of exclosures, years and seasons was significant. No significant yearly differences were found in Kochia utilization. The analysis reflects the greater overall variability in utilization of individual plants.

Data from Table 19 have been further summarized on the basis of area (Table 22). Note that the biomass values are fresh weight and that the total biomass fluctuations parallel the individual plant data, since rooting density of plants changed insignificantly during the study period. Removal values are the percentage of the standing crop that was browsed from the plants during that sampling period.

Browsing removed less than 0.1 percent to 15.1 percent of the Kochia biomass and 0.0 percent to 1.9 percent of the Sitanion. Mean removal of Kochia biomass was 3.71 percent (+ 2.88, SE) for winter samples. Removal of Sitanion biomass averaged 0.89 percent (+ 0.25, SE) for all samples.

These results agree with the observations that herbivory in shrub-steppe ecosystems removes less than 10 percent of net primary production (Petrusewicz and Grodzinski 1975). Shinn et al. (1975) and MacMahon et al. (1976) found herbivory removed less than 10 percent in both Atriplex confertifolia and Artemisia tridentata on the Biome Validation Site in Curlew Valley. Shinn et al. (1975) suggested that herbivory may be a randomly occurring episodic event of large
Table 21. Analyses of variance of arcsine transformed unweighted mean utilization per plant on plots sampled in livestock proof exclosures during 1976 to 1978 in Curlew Valley, Utah.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Kochia</th>
<th></th>
<th></th>
<th>Sitamon</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>F</td>
<td>Significance</td>
<td>MS</td>
<td>F</td>
<td>Significance</td>
</tr>
<tr>
<td>Total</td>
<td>287</td>
<td>0.1802</td>
<td>8.9652</td>
<td>$p \leq 0.005$</td>
<td>0.0797</td>
<td>5.0443</td>
<td>$p \leq 0.05$</td>
</tr>
<tr>
<td>Exclosure</td>
<td>1</td>
<td>0.0201</td>
<td>0.0211</td>
<td>NS$^a$</td>
<td>0.0609</td>
<td>8.0000</td>
<td>$p \leq 0.005$</td>
</tr>
<tr>
<td>Plots (Excl.)</td>
<td>46</td>
<td>0.04878</td>
<td>51.3147</td>
<td>$p \leq 0.001$</td>
<td>0.0319</td>
<td>5.5132</td>
<td>$p \leq 0.05$</td>
</tr>
<tr>
<td>Year</td>
<td>1</td>
<td>0.2116</td>
<td>22.7737</td>
<td>$p \leq 0.001$</td>
<td>0.0228</td>
<td>0.3684</td>
<td>NS</td>
</tr>
<tr>
<td>Season</td>
<td>2</td>
<td>0.1332</td>
<td>14.0211</td>
<td>$p \leq 0.001$</td>
<td>0.0070</td>
<td>0.269</td>
<td>$p \leq 0.05$</td>
</tr>
<tr>
<td>Year $\times$ Seas.</td>
<td>2</td>
<td>0.5500</td>
<td>57.8947</td>
<td>$p \leq 0.001$</td>
<td>0.0957</td>
<td>0.7500</td>
<td>NS</td>
</tr>
<tr>
<td>Excl. $\times$ Year</td>
<td>1</td>
<td>0.0507</td>
<td>5.3368</td>
<td>$p \leq 0.01$</td>
<td>0.0760</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Excl. $\times$ Seas.</td>
<td>2</td>
<td>0.0995</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>230</td>
<td>0.0095</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^a$ NS signifies $p > 0.05$. 
Table 22. Estimates of total standing crop biomass and total removal of Kochia americana and Sitanion hystrix in 1977 to 1978 on two exclosures in Curlew Valley, Utah.

<table>
<thead>
<tr>
<th>Sampling date</th>
<th>Species</th>
<th>Standing crop biomass (kg/ha)</th>
<th>Percentage removal</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>North</td>
<td>South</td>
</tr>
<tr>
<td>February 1977</td>
<td>Kochia sp.</td>
<td>134.52</td>
<td>37.30</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>102.80</td>
<td>21.62</td>
</tr>
<tr>
<td>June 1977</td>
<td>Kochia sp.</td>
<td>77.10</td>
<td>71.64</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>49.85</td>
<td>19.51</td>
</tr>
<tr>
<td>September 1977</td>
<td>Kochia sp.</td>
<td>69.25</td>
<td>40.63</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>124.37</td>
<td>19.82</td>
</tr>
<tr>
<td>February 1978</td>
<td>Kochia sp.</td>
<td>48.39</td>
<td>74.12</td>
</tr>
<tr>
<td></td>
<td>Sitanion sp.</td>
<td>58.85</td>
<td>11.03</td>
</tr>
</tbody>
</table>

\( ^a \) T indicates removal of less than 0.1 percent.
magnitude, based on observations that individual *Atriplex confertifolia* plants were sometimes 33 to 67 percent clipped by jackrabbits. The data on the individual plants from this study confirm the view of these workers.

Browsing of *Kochia* plants (Table 19) was compared during the last three sampling periods to estimates derived from transects located randomly throughout Curlew Valley (Table 23).

### Table 23. Mean percentage of *Kochia* plants browsed in randomly chosen samples of 100 plants located throughout the Curlew Valley jackrabbit study area.

<table>
<thead>
<tr>
<th>Sampling date</th>
<th>Number of transects</th>
<th>Mean percentage ± S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>June 1977</td>
<td>14</td>
<td>3.14 ± 0.79</td>
</tr>
<tr>
<td>September 1977</td>
<td>12</td>
<td>5.75 ± 1.25</td>
</tr>
<tr>
<td>February 1978</td>
<td>7</td>
<td>7.86 ± 1.94</td>
</tr>
</tbody>
</table>

Mean percentages of plants browsed on the transects were similar to exclosure values (Wilcoxon two sample test, $t_s = 1.21$, $p > 0.05$). Seasonal trends seemed to correspond to the exclosure samples with winter browsing higher than that of other seasons. This supports the assumption that the exclosures were representative of valley-wide utilization of *Kochia* by jackrabbits.
RESULTS OF MODEL STUDIES

Validation

Nutrition submodel

Once verification was complete, validation runs were made and output compared with field and literature data. Validation tests consisted of; (1) comparison of simulated adult body weight with the data of Stoddart (1972 and unpublished), (2) comparison of simulated milk production and juvenile growth with published data, and (3) comparison of energy and protein requirements with data from Nagy et al. (1976) and Shoemaker et al. (1976) for black-tailed jackrabbits.

Comparison of simulated body weight with the data of Stoddart (1972) was important as a test of the nutrition submodel's validity, since body weight changes reflect changes in physiological condition. In Figure 15 the results of validation runs using control inputs are plotted with measured average body weight data from Stoddart (1972) for 1964-1967. Male and female simulated body weights satisfy the validation criterion of passing through the 95 percent confidence intervals 80 percent of the time. Simulated weight of males (lower two curves) does not decrease as much during the breeding season as do observed values. As a result the model overestimates body weight later in the year. Female body weights (upper two curves) remain within the error bars except during the later part of the breeding
Figure 15. Validation simulation of annual body weight dynamics of jackrabbits compared with measured body weights from 1964 to 1967. Error bars are 95 percent confidence limits.

--1-- Simulated adult male weights
--2-- Simulated adult female weights
3-3-3 Measured adult male weights
4-4-4 Measured adult female weights
season. Simulated weights for females drop much more quickly than is observed during this period, suggesting the need for further model refinement.

Adult male and female body weight curves are nearly mirror images of one another during the breeding season. Female weights increase as a result of pregnancy and lactation while male weights decrease. Model mechanisms accounting for this difference include changes in intake and activity patterns. The increase in body weights for females during pregnancy and lactation is well known (Maynard and Loosli 1969, Vander et al. 1970) but no firm explanation can be offered for the male body weight changes.

Jackrabbit density in 1964 to 1967 in Curlew Valley (Gross et al. 1974) was relatively low. Nutrition submodel output was compared to data for years of increasing and relatively high population densities (1968-1972). Figure 16 shows simulation results for females compared to average observed body weights for this period. Model output (Figure 16) is satisfactory but fails to meet the validation criterion and the observed female body weight changes appear more erratic and variable than during low density years (Figure 15). Male body weight changes are more similar to years of low population densities (Figure 17) and the model again fails to reach the low point of observed body weights.

The pattern of simulated milk production (Figure 18) during the lactation period agrees well with that observed for domestic animals (Maynard and Loosli 1969) and white-tailed deer (Moen 1973). At
Figure 16. Simulated adult female body weight dynamics over an annual cycle. Error bars are 95 percent confidence intervals.

-1- Simulated adult female weights
2-2-2 Measured adult female weights using 1968 to 1972 data
Figure 17. Simulated adult male body weight dynamics over an annual cycle. Error bars are 95 percent confidence limits on measured values.

-1-1- Simulated adult male weights
2-2-2 Measured adult male weights using 1968 to 1972 data
Figure 18. Simulated daily milk production (g/day) for lactating jackrabbits with a litter of five young.
the peak of lactation the model predicts that the female would be producing approximately 195 g of milk per day. Cook (1972) estimated that maximum milk production for black-tailed jackrabbits would be about 170 g/day.

The daily milk production simulated by the model is shown in Figure 19 for litters of sizes 2, 5, 7, and 5 young. Since milk production is a function of demand by the offspring, estimated demand for milk to sustain maximum juvenile growth is high for large litters. If energy intake is restricted for any reason or if forage is of poor quality, simulated daily milk production is reduced (Figure 20). This might occur if forage intake was reduced because of drier herbage. The restriction in milk produced then causes reduced growth rates of the young. This point will be further expanded later.

Figure 21 shows the results of simulated growth of juveniles from a litter born on day 21. The upper curve is the simulated potential growth based on the data of Haskell and Reynolds (1947). The lower curve represents growth in the model and deviates slightly from potential growth. The model output lags the potential growth curve early and thereafter remains under potential growth.

Simulated average body weight for individuals in each of four litters produced is shown in Figure 22 where data and initial conditions were those of the high density years of 1968 to 1972. Litters three and four failed to achieve potential growth, reaching only 75 and 88 percent respectively of their year-end potential body weights. If severe restrictions are placed on the nutrition of the female, greater lags occur, as shown in Figure 23. In this case the litter
Figure 19. Simulated annual daily milk production (g/day) for jackrabbits producing four litters in a year.

--- Simulated daily demand for maximum sustained juvenile growth
--2-- Simulated daily production of milk
---C--- Common points
Figure 20. Simulated daily milk production by lactating jackrabbits with a third litter of seven young.

- - Simulated daily demand for maximum sustained growth
--2-- Simulated production of milk
Figure 21. Simulated growth of first litter juveniles.

-1- Simulated results of realized growth
-2- Simulated potential growth curve based on data of Haskell and Reynolds (1947)
Figure 22. Simulated body growth of four successive litters, during high density years.
Figure 23. Simulation of the growth of the third litter (parturition date = day 109).

-1-1- Simulated results of realized growth
-222- Simulated potential growth curve based on date of Haskell and Reynolds (1947)
only reached 66 percent of its potential final weight. It should be emphasized that potential growth is based on hand-reared, captive animals and it is difficult to interpret these reductions relative to natural populations. Restricted growth of up to 50 percent may have little effect on survival (Brody 1945, Kleiber 1961).

Since body weights are influenced by many factors in the model, additional support was sought for model validity from predicted energy and nitrogen requirements. Average energy requirements per kilogram of body weight were taken from 15-30 January and 15-30 July. Mean values were then calculated from 10 runs of the model with parameters selected randomly. For the winter period, the mean model estimate of daily energy requirement was 161.23 kcal/kg/day (± 6.12, SE) compared to the empirical measure of 172.00 kcal/kg/day for black-tailed jackrabbits in winter (Shoemaker et al. 1976). The mean model estimate in the summer period was 129.57 kcal/kg/day (± 5.92, SE), compared to 142 kcal/kg/day measured by Shoemaker et al. (1976).

Daily nitrogen requirements averaged 353.60 mg/kg/day (± 20.13, SE) of required nitrogen for 10 runs of the winter and summer periods combined. The model estimate compares to 330-450 mg/kg/day measured by Nagy et al. (1976) on black-tailed jackrabbits and 375 mg/kg/day reported by Holter et al. (1974) for snowshoe hares.

Population submodel

The population model could not be validated in the same sense as the nutrition submodel because; (1) all available data were used to build the submodel and would have had to be used to validate it, and
specific causes of mortality other than predation have not been identified. The submodel was checked for reasonableness and completeness so that it was assumed that model experiments would be valid.

Figure 24 shows the output of one run of the model made with the demographic inputs from 1976. Adult mortality during the summer appears to be zero but this is an artifact of the plotting routine. The rapid changes in the density of subadults are due to the recruitment of each litter which occurs in a single day.

Average daily mortality rate of adults during the winter, as calculated from the model output, is 0.010043 which is 78 percent mortality for a winter period of 150 days. The model value compares with the observed value of 78 percent mortality for the 1975-1976 winter (Stoddart 1977).

April to October adult mortality observed by Stoddart (1977) in 1976 was 0 percent. Average daily mortality rate modeled for the same period was 0.000219, or 4.6 percent mortality, using 213 days for the April to October period.

Modeled juvenile mortality, from birth to October, a period of approximately 180 days, was 0.000416 per day which is equivalent to 7.2 percent, compared to the 7 percent calculated by Stoddart (1977) for juveniles during 1976.

The close agreement of the mortality estimates results because most of the modeled mortality was attributed to predation which was input and not modified by nutritional condition. Nutritionally related mortality was insignificant except for the summer, when nutrition-caused mortality increased slightly, especially for adult
Figure 24. Simulated density of adults (++) and subadults (2-2) in 1976.
females. The modeled age ratio of 13 percent adults in the fall compares well with the value of 15 percent adults that Stoddart (1977) calculated for 1976.

The fate of individual litters for the same inputs as the above run is shown in Figure 25. Parturition occurred on days 60, 99, and 138 of this run and each litter suffered similar mortality after birth. It was thought that mortality rates might be greater between birth and weaning (because of nutritional stress), but the model mechanisms did not predict this differential mortality.

A few runs of more than 1 year duration were made with the model. These runs were driven with average environmental conditions for increasing or high years (1968-1972) and for low years (1966-1967, 1973-1975) and yearly natality and mortality inputs. Table 24 presents population density and age ratio output for a run covering the years 1966 to 1975. The model population was "censused" on day 81 (spring, pre-breeding population) and day 291 (fall population) and density is in individuals per square kilometer. The Curlew Valley population reached a low fall population of approximately 12 jackrabbits/km\(^2\) in 1967 and peaked at approximately 102 jackrabbits/km\(^2\) in the fall of 1970. The model fall population had already begun a slight increase in 1967 but peaked at about the same time as the real population. Model age ratios correspond well with the observed age ratios.

These population submodel runs do not substantiate the model mechanisms used but serve to show that the submodel is a realistic representation of the system.
Figure 25. Simulated density of three litters of subadults during 1976.
Table 24. Population submodel output for the simulated period of 1966 to 1975. Population density is given in individuals/km².

<table>
<thead>
<tr>
<th>Year</th>
<th>Spring population</th>
<th>Fall population</th>
<th>Proportion of adults in fall</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Model</td>
</tr>
<tr>
<td>1966</td>
<td>5.89</td>
<td>11.83</td>
<td>0.15</td>
</tr>
<tr>
<td>1967</td>
<td>4.11</td>
<td>15.98</td>
<td>0.16</td>
</tr>
<tr>
<td>1968</td>
<td>6.63</td>
<td>42.14</td>
<td>0.14</td>
</tr>
<tr>
<td>1969</td>
<td>27.48</td>
<td>74.34</td>
<td>0.15</td>
</tr>
<tr>
<td>1970</td>
<td>38.75</td>
<td>107.21</td>
<td>0.27</td>
</tr>
<tr>
<td>1971</td>
<td>59.00</td>
<td>83.13</td>
<td>0.36</td>
</tr>
<tr>
<td>1972</td>
<td>36.03</td>
<td>26.60</td>
<td>0.46</td>
</tr>
<tr>
<td>1973</td>
<td>7.82</td>
<td>6.79</td>
<td>0.16</td>
</tr>
<tr>
<td>1974</td>
<td>1.94</td>
<td>8.85</td>
<td>0.20</td>
</tr>
<tr>
<td>1975</td>
<td>1.79</td>
<td>7.07</td>
<td>0.19</td>
</tr>
</tbody>
</table>
Sensitivity

Sensitivity analyses (Wiens and Innis 1974) in the form of altering model parameters and input variables one at a time noting changes in selected output variables, was done to examine model properties. Each submodel was treated separately so that tests could be more detailed and efficient in examining properties of submodels (Caswell 1976). Whole model sensitivity was examined by way of variation in output for stochastically chosen parameters. This sensitivity analysis was done to estimate the number of model runs needed for statistical comparisons when conducting model experiments.

Nutrition submodel

A control run using low density initial conditions and the average body weight data of 1964 and 1967 was defined. The ratio of output change to input change is given in Table 25 for a variety of sensitivity indicators and input variable or parameter alterations. Body weights were chosen as indicators because they reflect physiological condition and auxiliary variables of energy and protein balance of females (EBF and PBF respectively) were chosen because of their importance in internal dynamics of the model. The negative sign of these variables reflects demand on the female at the critical time of peak lactation.

Table 25 shows that for many cases output changed little (e.g., weight of adult males, WADM). Changing timing parameter for growth (IBRK) and temperature acclimization (ITT), or critical temperatures
Table 25. Summary of the effects of altering submodel parameters on estimates of selected variables of the nutrition submodel. Alterations are expressed as percentages of the control values. The sensitivity is measured as the fraction change in output divided by the fraction change in input.

<table>
<thead>
<tr>
<th>Altered parameter</th>
<th>Nature of alteration</th>
<th>Magnitude of alteration</th>
<th>Post-breeding WADD</th>
<th>Post-breeding WADF</th>
<th>Peak lactation EBF</th>
<th>Peak lactation PBF</th>
<th>Oct. 1 WUJUV(1)</th>
<th>Oct. 1 WUJUV(2)</th>
<th>Oct. 1 WUJUV(3)</th>
<th>Oct. 1 WUJUV(4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>None</td>
<td>None</td>
<td>2.041&lt;sup&gt;C&lt;/sup&gt;</td>
<td>2.290</td>
<td>-62.89</td>
<td>-25.85</td>
<td>2.012</td>
<td>1.845</td>
<td>1.050</td>
<td>0.759</td>
</tr>
<tr>
<td>HP1</td>
<td>Lower summer Tc increased to 28.6°C</td>
<td>+ 10%</td>
<td>0.00&lt;sup&gt;d&lt;/sup&gt;</td>
<td>-0.53</td>
<td>-0.08</td>
<td>-0.13</td>
<td>0.01</td>
<td>-0.07</td>
<td>-0.05</td>
<td>0.59</td>
</tr>
<tr>
<td>HP6</td>
<td>Upper summer Tc decreased to 31.6°C</td>
<td>- 10%</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>HP9</td>
<td>Lower winter Tc increased to 23.1°C</td>
<td>+ 10%</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>HP12</td>
<td>Upper winter Tc decreased to 25.2°C</td>
<td>- 10%</td>
<td>0.00</td>
<td>0.21</td>
<td>2.03</td>
<td>1.10</td>
<td>-0.01</td>
<td>0.13</td>
<td>0.10</td>
<td>-0.43</td>
</tr>
<tr>
<td>GAINC</td>
<td>Activity increment increased to 0.44</td>
<td>+ 10%</td>
<td>0.02</td>
<td>-0.60</td>
<td>0.93</td>
<td>0.51</td>
<td>-0.02</td>
<td>-0.15</td>
<td>-0.36</td>
<td>0.07</td>
</tr>
<tr>
<td>GAINC</td>
<td>Activity increment decreased to 0.36</td>
<td>- 10%</td>
<td>0.00</td>
<td>0.24</td>
<td>0.31</td>
<td>0.37</td>
<td>0.00</td>
<td>0.02</td>
<td>0.03</td>
<td>-0.61</td>
</tr>
<tr>
<td>BAL</td>
<td>Energy balance point decreased to 0.01</td>
<td>- 90%</td>
<td>0.00</td>
<td>0.02</td>
<td>0.03</td>
<td>0.01</td>
<td>0.00</td>
<td>0.01</td>
<td>0.02</td>
<td>-0.03</td>
</tr>
<tr>
<td>STOR</td>
<td>Stored reserves used increased to 0.20</td>
<td>+ 33%</td>
<td>0.00</td>
<td>-0.34</td>
<td>-0.59</td>
<td>0.18</td>
<td>0.00</td>
<td>-0.03</td>
<td>0.05</td>
<td>0.18</td>
</tr>
<tr>
<td>STOR</td>
<td>Stored reserves used decreased to 0.10</td>
<td>- 33%</td>
<td>0.00</td>
<td>-0.11</td>
<td>-0.78</td>
<td>0.18</td>
<td>0.00</td>
<td>0.02</td>
<td>0.08</td>
<td>0.03</td>
</tr>
<tr>
<td>CY</td>
<td>Young potential growth rate increased to 0.018857</td>
<td>+ 10%</td>
<td>0.00</td>
<td>-0.47</td>
<td>-1.03</td>
<td>-1.22</td>
<td>0.58</td>
<td>0.49</td>
<td>0.41</td>
<td>1.20</td>
</tr>
<tr>
<td>CY</td>
<td>Young potential growth rate decreased to 0.015429</td>
<td>- 10%</td>
<td>0.00</td>
<td>0.05</td>
<td>-1.01</td>
<td>-1.10</td>
<td>0.57</td>
<td>0.57</td>
<td>0.50</td>
<td>0.58</td>
</tr>
<tr>
<td>CJ</td>
<td>Juvenile potential growth rate increased to 0.011</td>
<td>+ 10%</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>-0.10</td>
<td>-0.05</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>CJ</td>
<td>Juvenile potential growth rate decreased to 0.009</td>
<td>- 10%</td>
<td>0.00</td>
<td>0.21</td>
<td>2.03</td>
<td>1.10</td>
<td>-0.09</td>
<td>0.11</td>
<td>0.12</td>
<td>-0.42</td>
</tr>
<tr>
<td>LINC</td>
<td>Lactation protein cost increased to 1.43</td>
<td>+ 10%</td>
<td>0.00</td>
<td>-0.01</td>
<td>-0.10</td>
<td>-0.86</td>
<td>0.97</td>
<td>-0.01</td>
<td>-0.09</td>
<td>-0.22</td>
</tr>
<tr>
<td>PINC</td>
<td>Pregnancy protein cost increased to 1.32</td>
<td>+ 10%</td>
<td>0.00</td>
<td>-0.49</td>
<td>0.25</td>
<td>0.30</td>
<td>-0.01</td>
<td>-0.08</td>
<td>-0.27</td>
<td>0.42</td>
</tr>
</tbody>
</table>
### Table 25. Continued.

<table>
<thead>
<tr>
<th>Altered parameter</th>
<th>Nature of alteration</th>
<th>Magnitude of alteration</th>
<th>Post-breeding WADG</th>
<th>Post-breeding WADG</th>
<th>Peak lactation EBF</th>
<th>Peak lactation PBF</th>
<th>Oct. 1 WJUV(1)</th>
<th>Oct. 1 WJUV(2)</th>
<th>Oct. 1 WJUV(3)</th>
<th>Oct. 1 WJUV(4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>CPD</td>
<td>Monthly crude protein digestibility increased</td>
<td>+ 10%</td>
<td>0.01</td>
<td>0.03</td>
<td>1.74</td>
<td>1.76</td>
<td>-0.01</td>
<td>-0.05</td>
<td>-0.31</td>
<td>-0.20</td>
</tr>
<tr>
<td>CPD</td>
<td>Monthly crude protein digestibility decreased</td>
<td>- 10%</td>
<td>0.00</td>
<td>-0.01</td>
<td>0.94</td>
<td>-1.16</td>
<td>-0.01</td>
<td>0.09</td>
<td>0.23</td>
<td>-0.15</td>
</tr>
<tr>
<td>CMAX</td>
<td>Maximum daily consumption decreased to 180 gms</td>
<td>- 25%</td>
<td>0.38</td>
<td>1.23</td>
<td>0.64</td>
<td>0.69</td>
<td>0.85</td>
<td>-1.03</td>
<td>-1.06</td>
<td>-1.15</td>
</tr>
<tr>
<td>CMAX</td>
<td>Maximum daily consumption decreased to 200 gms</td>
<td>- 17%</td>
<td>0.12</td>
<td>1.14</td>
<td>0.20</td>
<td>0.32</td>
<td>0.49</td>
<td>-1.00</td>
<td>-1.07</td>
<td>-1.01</td>
</tr>
<tr>
<td>CMAX</td>
<td>Maximum daily consumption decreased to 220 gms</td>
<td>- 8%</td>
<td>0.00</td>
<td>0.31</td>
<td>0.91</td>
<td>0.44</td>
<td>0.19</td>
<td>0.75</td>
<td>0.69</td>
<td>0.15</td>
</tr>
<tr>
<td>AHI</td>
<td>Heat increment increased to 0.44</td>
<td>+ 10%</td>
<td>0.00</td>
<td>-0.52</td>
<td>-0.37</td>
<td>-0.30</td>
<td>0.01</td>
<td>-0.12</td>
<td>-0.40</td>
<td>0.26</td>
</tr>
<tr>
<td>FDIM</td>
<td>Food intake parameter increased to 0.022</td>
<td>+ 10%</td>
<td>0.01</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.01</td>
<td>-0.07</td>
<td>-0.18</td>
<td>0.26</td>
</tr>
<tr>
<td>FDIM</td>
<td>Food intake parameter decreased to 0.018</td>
<td>- 10%</td>
<td>0.03</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.01</td>
<td>0.07</td>
<td>0.08</td>
<td>-0.57</td>
</tr>
<tr>
<td>FDIF</td>
<td>Food intake parameter increased to 0.022</td>
<td>+ 10%</td>
<td>0.01</td>
<td>-0.40</td>
<td>0.85</td>
<td>0.56</td>
<td>-0.01</td>
<td>-0.12</td>
<td>-0.27</td>
<td>0.12</td>
</tr>
<tr>
<td>FDIF</td>
<td>Food intake parameter decreased to 0.018</td>
<td>- 10%</td>
<td>0.00</td>
<td>0.40</td>
<td>0.91</td>
<td>0.58</td>
<td>0.00</td>
<td>0.03</td>
<td>-0.18</td>
<td>-0.42</td>
</tr>
<tr>
<td>IBRK</td>
<td>Timing of growth parameter changes delayed to day 77</td>
<td>+ 10%</td>
<td>0.33</td>
<td>-0.13</td>
<td>-0.12</td>
<td>0.00</td>
<td>0.00</td>
<td>0.25</td>
<td>0.28</td>
<td>0.26</td>
</tr>
<tr>
<td>IBRK</td>
<td>Timing of growth parameter changes made earlier than day 63</td>
<td>- 10%</td>
<td>0.12</td>
<td>-0.12</td>
<td>0.00</td>
<td>0.00</td>
<td>0.22</td>
<td>0.25</td>
<td>0.20</td>
<td>0.30</td>
</tr>
<tr>
<td>ITT</td>
<td>Earlier loss of winter temperature acclimation day 130</td>
<td>- 13%</td>
<td>0.03</td>
<td>0.13</td>
<td>1.58</td>
<td>0.85</td>
<td>-0.01</td>
<td>0.14</td>
<td>0.09</td>
<td>-0.32</td>
</tr>
<tr>
<td>0</td>
<td>Monthly digestible energy increased</td>
<td>+ 10%</td>
<td>0.01</td>
<td>0.39</td>
<td>1.91</td>
<td>0.54</td>
<td>0.07</td>
<td>0.21</td>
<td>1.79</td>
<td>0.85</td>
</tr>
<tr>
<td>0</td>
<td>Monthly digestible energy decreased</td>
<td>- 10%</td>
<td>-0.01</td>
<td>0.65</td>
<td>-0.21</td>
<td>-0.76</td>
<td>0.16</td>
<td>0.79</td>
<td>0.28</td>
<td>0.67</td>
</tr>
</tbody>
</table>
Table 25. Continued

<table>
<thead>
<tr>
<th>Altered parameter</th>
<th>Nature of alteration</th>
<th>Magnitude of alteration</th>
<th>Post-breeding(^a) WADM</th>
<th>Post-breeding(^a) WADF</th>
<th>Peak lactation(^b) EBF</th>
<th>Peak lactation PBF</th>
<th>Oct. 1 WJUV(^c)(1)</th>
<th>Oct. 1 WJUV(^c)(2)</th>
<th>Oct. 1 WJUV(^c)(3)</th>
<th>Oct. 1 WJUV(^c)(4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>TWN1</td>
<td>Earlier weaning beginning day 5</td>
<td>- 29%</td>
<td>0.00</td>
<td>0.05</td>
<td>0.40</td>
<td>0.65</td>
<td>0.00</td>
<td>0.03</td>
<td>0.10</td>
<td>-0.03</td>
</tr>
<tr>
<td>TWN2</td>
<td>Later weaning ending day 28</td>
<td>+ 33%</td>
<td>0.00</td>
<td>-0.17</td>
<td>0.09</td>
<td>-0.59</td>
<td>-0.11</td>
<td>-0.18</td>
<td>-0.43</td>
<td>-0.13</td>
</tr>
<tr>
<td>DT</td>
<td>Time step changed to DT = 3 days</td>
<td>+ 300%</td>
<td>0.00</td>
<td>-0.13</td>
<td>-0.31</td>
<td>-0.45</td>
<td>-0.05</td>
<td>-0.14</td>
<td>-0.15</td>
<td>-0.13</td>
</tr>
</tbody>
</table>

\(^a\) Post-breeding = day 241.  
\(^b\) Peak of lactation = day 156.  
\(^c\) Control run output; WADM, WADF, WJUV (kg/indiv.); EBF (kcal/indiv.+day); PBF (g CP/indiv.+day).  
\(^d\) 0.00 = no effect of input change; 1.00 = equal effect as input change; + ratio = output change in same direction as input change; and - ratio = output change in opposite direction from input change.
(HP3, HP6, HP9), had little effect on any sensitivity indicator. In some cases, the sensitivity ratio was much greater than 1.0, indicating greater sensitivity to parameter or input change than might have been anticipated. Many of the indicator changes are in opposite directions to parameter changes (indicated by negative sign of the sensitivity ratio). Some of these are easy to understand biologically, for example, the lowered activity increment (GAINC) resulting in positive changes in the weight and energy and protein balance of adult females. Others are difficult to explain, like the negative response of the female energy balance when protein costs of lactation (LINC) are increased and the complex nonlinearities of the model structure are reflected.

The effects of alterations of constants and input variables that are most subject to error are of interest, for example digestible energy and protein, the maximum consumption rate, and food intake rate parameters. Increases in digestible energy (D) have a large effect on energy balance of females at the peak of lactation. Digestible energy changes also increase the October 1 body weights of juveniles. Increases in crude protein digestibility (CPD) benefit energy and protein balance of the lactating females. Changes in food intake parameters for males (FDIM) have little effect and changes in food intake parameters of females (FDIF) have moderate effect. These parameters were estimated from "tuning" runs and are subject to substantial error.

Since there are such a wide variety of estimates of maximum consumption (CMAX) in the literature, sensitivity of the parameter
is important. Based on published values (particularly those of Shoe-maker et al. 1976) I felt that CMAX may have been overestimated. Small reductions in CMAX have moderate effects, increasing the October 1 body weights of juveniles. Energy and protein balance responded positively to CMAX reductions because young demand for milk was reduced as young were weaned more quickly. Other responses are of about the same order as the parameter alteration, leading to the conclusion that submodel dynamics are not unusually sensitive to errors in this parameter. Sensitivity analysis results support the structural soundness of the nutrition submodel.

Population submodel

Sensitivity tests similar to those made on the nutrition submodel were conducted on the population submodel. In these tests (Table 26) the control run used 1976 demographic data and corresponding inputs for a low density situation. Density of the sex and age classes was used as the sensitivity indicator since these affect forage consumption and nutrition through availability, and unexpected variation could affect experimental runs.

The submodel was sensitive to changes in instantaneous mortality rates for all seasons, with input changes producing output changes of nearly the same magnitude (sensitivity indicator = 1.0). Of course, higher mortality rates produce lower populations so the indicator is negative. Altering summer (April-October) mortality rates of adults (CASMNT, CASMPD) affected the density of juveniles since their density is dependent upon the number of breeding females.
Table 26. Summary of the effects of altering submodel parameters on estimates of selected variables of the population submodel. Alterations are expressed as percentages of control values. The sensitivity is measured as the fraction change in output divided by the fraction change in input.

<table>
<thead>
<tr>
<th>Altered parameter</th>
<th>Nature of alteration</th>
<th>Magnitude of alteration</th>
<th>Post-breeding $^a$</th>
<th>Post-breeding $^b$</th>
<th>Oct. 1 DJUV(1)</th>
<th>Oct. 1 DJUV(2)</th>
<th>Oct. 1 DJUV(3)</th>
<th>Oct. 1 DJUV(4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>None</td>
<td>None</td>
<td>0.0068 $^c$</td>
<td>0.0065</td>
<td>0.0126</td>
<td>0.0327</td>
<td>0.0308</td>
<td>0.0185</td>
</tr>
<tr>
<td>PREMOR</td>
<td>Prenatal mortality increased constant = 0.0028.</td>
<td>+ 10%</td>
<td>0.00 $^c$</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>-0.01</td>
</tr>
<tr>
<td>PREMOR</td>
<td>Prenatal mortality decreased constant = 0.0023.</td>
<td>- 10%</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.01</td>
</tr>
<tr>
<td>CWMMAT</td>
<td>Natural mortality in winter increased constant = 0.418</td>
<td>+ 10%</td>
<td>-0.90</td>
<td>-0.90</td>
<td>-0.05</td>
<td>-0.03</td>
<td>-0.06</td>
<td>-0.07</td>
</tr>
<tr>
<td>CWMMAT</td>
<td>Natural mortality in winter decreased constant = 0.342</td>
<td>- 10%</td>
<td>0.90</td>
<td>0.90</td>
<td>0.05</td>
<td>0.04</td>
<td>0.06</td>
<td>0.07</td>
</tr>
<tr>
<td>CWMPRO</td>
<td>Predation mortality in winter increased constant = 1.078</td>
<td>+ 10%</td>
<td>-1.00</td>
<td>-1.00</td>
<td>-0.10</td>
<td>-0.12</td>
<td>-0.13</td>
<td>-0.13</td>
</tr>
<tr>
<td>CWMPRO</td>
<td>Predation mortality in winter decreased constant = 0.882</td>
<td>- 10%</td>
<td>1.00</td>
<td>1.00</td>
<td>0.10</td>
<td>0.12</td>
<td>0.13</td>
<td>0.13</td>
</tr>
<tr>
<td>CASMNT</td>
<td>Natural mortality in summer increased constant = 0.100</td>
<td>+ 10%</td>
<td>-1.00</td>
<td>-1.00</td>
<td>-0.55</td>
<td>-0.50</td>
<td>-0.48</td>
<td>-0.58</td>
</tr>
<tr>
<td>CASMPO</td>
<td>Predation mortality in summer increased constant = 0.873</td>
<td>+ 10%</td>
<td>1.01</td>
<td>-1.02</td>
<td>-0.90</td>
<td>-0.92</td>
<td>-0.95</td>
<td>-1.00</td>
</tr>
<tr>
<td>CASMPO</td>
<td>Predation mortality in summer decreased constant = 0.715</td>
<td>- 10%</td>
<td>1.00</td>
<td>1.03</td>
<td>0.91</td>
<td>0.92</td>
<td>0.95</td>
<td>0.99</td>
</tr>
<tr>
<td>CJMMAT</td>
<td>Natural mortality of juveniles increased constant = 0.528</td>
<td>+ 10%</td>
<td>0.00</td>
<td>0.00</td>
<td>-1.00</td>
<td>-1.01</td>
<td>-1.00</td>
<td>-1.02</td>
</tr>
<tr>
<td>CJMMAT</td>
<td>Natural mortality of juveniles decreased constant = 0.432</td>
<td>- 10%</td>
<td>0.00</td>
<td>0.00</td>
<td>1.00</td>
<td>1.01</td>
<td>1.00</td>
<td>1.03</td>
</tr>
</tbody>
</table>
Table 26. Continued.

<table>
<thead>
<tr>
<th>Altered parameter</th>
<th>Nature of alteration</th>
<th>Magnitude of alteration</th>
<th>Post-breeding&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Post-breeding</th>
<th>Oct. 1</th>
<th>Oct. 1</th>
<th>Oct. 1</th>
<th>Oct. 1</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>DAOM</td>
<td>DADF</td>
<td>DJUV(1)</td>
<td>DJUV(2)</td>
<td>DJUV(3)</td>
<td>DJUV(4)</td>
</tr>
<tr>
<td>CJMPRO</td>
<td>Predation mortality of juveniles increased constant = 1.970</td>
<td>+10%</td>
<td>0.00</td>
<td>0.00</td>
<td>-1.01</td>
<td>-0.99</td>
<td>-1.02</td>
<td>-1.00</td>
</tr>
<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Predation mortality of juveniles decreased constant = 1.612</td>
<td>-10%</td>
<td>0.00</td>
<td>0.00</td>
<td>1.01</td>
<td>0.99</td>
<td>1.02</td>
<td>1.00</td>
</tr>
<tr>
<td></td>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SEXR</td>
<td>Fraction of males increased constant = 0.55.</td>
<td>+10%</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
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<tr>
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<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CDEN</td>
<td>Food competition density increased constant = 0.319.</td>
<td>+10%</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>CDEN</td>
<td>Food competition density decreased constant = 0.261.</td>
<td>-10%</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>PREG</td>
<td>Pregnancy rates all decreased.</td>
<td>-10%</td>
<td>0.00</td>
<td>0.00</td>
<td>-0.80</td>
<td>-0.87</td>
<td>-0.90</td>
<td>-0.98</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SF1</td>
<td>Asymptote of survival function increased constant = 1.155</td>
<td>+10%</td>
<td>1.00</td>
<td>1.00</td>
<td>1.00</td>
<td>1.02</td>
<td>1.00</td>
<td>1.00</td>
</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SF1</td>
<td>Asymptote of survival function decreased constant = 0.945</td>
<td>-10%</td>
<td>-1.00</td>
<td>-1.00</td>
<td>-1.00</td>
<td>-1.00</td>
<td>-1.00</td>
<td>-1.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SF2</td>
<td>Intercept of survival function increased constant = 33.0.</td>
<td>+10%</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SF3</td>
<td>Inflection point of survival function increased constant = 11.0</td>
<td>+10%</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
</tbody>
</table>

<sup>a</sup> Post-breeding = day 241.

<sup>b</sup> Control run output; DAOM, DADF, DJUV (no./he).

<sup>c</sup> 0.00 = no effect of input change; 1.00 = equal effect to input change; + ratio = output change in same direction as input change; and - ratio = output change in opposite direction from input change.
Ten percent changes in prenatal mortality (PREMOR) had little effect on dynamics. Decreases in pregnancy rates produced lower juvenile densities.

Density was sensitive to changes in the asymptote (SF1) of the survival function, being increased or decreased by the same percentage as the alteration. The submodel was not sensitive to changes in parameters controlling the intercept or inflection point of the function (SF2, SF3). This insensitivity arises because energy and protein deficiency occur for few days during a run.

Model stochastic properties

Multiple runs of the jackrabbit model with parameters selected randomly produced a mean and standard deviation for each state variable. Numerous stochastic runs were made to select design for model experimentation. These runs produced estimates of output variation as a function of randomly chosen parameters. Coefficients of variation (CV = 100s/x) for all parameters and input variables averaged 39 percent (n = 104 parameters and input variables), ranging from 5 to 300 percent. Variation in output body weights, especially of adults, was smallest. CV of weights of adult males was 2.8 percent and of adult females was 9.7 percent. Weights of juveniles were more variable with an average CV for four litters of 19.3 percent. Density was more variable with CV averaging 24.9 percent for all sex and age classes. State variables were less variable (mean CV about 20 percent) than were parameters and input variables.

The CV of energy balance of females was 62 percent and of protein balance was 61 percent. The importance to the model of these results
is that these variables are affected by nutritional relationships and are key links between submodels. With such variation model output was consistent enough to be used in model experiments. The relatively moderate effects of these stochastic alterations reflect the feedback loops and homeostasis of the modeled nutritional/physiological system.

**Model Experiments**

After verification, validation, and sensitivity analyses were complete, the model was used to test four study hypotheses. The "biological" tests of significance involved running the model under various conditions and using judgement about the likelihood of the results. This kind of test was used to examine H(2) and H(7) (see Table 1). Other model experiments were of the more familiar "statistical" type, for H(5) and H(6).

**Forage requirements**

Modeled forage requirements of jackrabbit populations were compared for low (1976) and high density years (1972). To estimate the likelihood of different results, comparisons were made with control conditions, in which digestion efficiency was reduced. Reducing digestible energy was selected for comparison because: (1) the empirical data base is good, and (2) the nutritional literature provides intuition about the likelihood of such reductions.

Under high density conditions, required forage (QUAN) was about five times that for low density (Table 27).
Table 27. Forage requirements of the jackrabbit population in model runs with different initial population densities. Required forage (QUAN, kg/ha/day) is expressed as a percentage (DEPl) of the available forage.

<table>
<thead>
<tr>
<th>Julian date</th>
<th>Low density (control)</th>
<th>High density</th>
<th>Treatments</th>
<th>Average reduction in digestible energy efficiency (percent)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>QUAN</td>
<td>DEPl</td>
<td>QUAN</td>
<td>DEPl</td>
</tr>
<tr>
<td></td>
<td>QUAN</td>
<td>DEPl</td>
<td>QUAN</td>
<td>DEPl</td>
</tr>
<tr>
<td>60 (Mar 1)</td>
<td>0.0031</td>
<td>0.06</td>
<td>0.0318</td>
<td>0.26</td>
</tr>
<tr>
<td>105 (Apr 15)</td>
<td>0.0024</td>
<td>0.04</td>
<td>0.0201</td>
<td>0.18</td>
</tr>
<tr>
<td>150 (Jun 1)</td>
<td>0.0074</td>
<td>0.14</td>
<td>0.0509</td>
<td>0.43</td>
</tr>
<tr>
<td>200 (Jul 1)</td>
<td>0.0104</td>
<td>0.18</td>
<td>0.0583</td>
<td>0.35</td>
</tr>
<tr>
<td>300 (Nov 1)</td>
<td>0.0163</td>
<td>0.31</td>
<td>0.0388</td>
<td>0.22</td>
</tr>
<tr>
<td>Means</td>
<td>0.0079</td>
<td>0.146</td>
<td>0.0400</td>
<td>0.288</td>
</tr>
</tbody>
</table>
During the breeding season (comparing April 15 values), over eight times as much forage was required. Even under the treatment of greatest reduction in digestible energy efficiency (57 percent reduction), the forage required was only about twice that of the low density (control) conditions. Such a drastic reduction in digestive efficiency is unlikely, thus suggesting that forage requirements at high density are significantly different than low density.

When required forage is measured as a percentage of available, the low density population required only about 0.146 percent of the available herbage to maintain normal population processes. The high density population required about 0.288 percent of the available forage. The ratio of required to available was nearly the same with 57 percent reduction in digestion efficiency. Therefore, although at high densities jackrabbits may be taking twice as much of the forage available when compared to low density, the forage that is removed is an insignificant part of the available forage.

These results show that jackrabbits do not require more forage than is available to the populations at high densities and thus H(2) cannot be rejected. Even if model results erred by an order of magnitude, the populations' requirements would not exceed 10 percent of available forage. Model results agree well with the exclosure studies (see Table 22), depicting similar levels of utilization of available forage. The model predicts lower removal because model experiments were based on the total forage available and the exclosure studies treated two palatable species.
Energy and protein balance

For nutritional relationships to impact population dynamics, energy and protein balances would have to be affected. To test this prediction (see Table 1, H(5) and H(6)) model experiments were conducted where these variables were examined at the peak of lactation for the largest litter and immediately prior to conception of the first litter. The period prior to breeding is affected by the over-winter nutritional regime. The model was run 40 times with randomly selected parameter values and energy and protein balances of the adult females were recorded for each period from each run. The treatments consisted of two densities (high and low) and two dietary inputs (those of the present study and those of Westoby (1973)). Two of the experimental blocks represent situations that have occurred in nature; my dietary data with low density jackrabbit populations and Westoby's dietary data with high populations. The other two situations (my dietary data/high density and Westoby's dietary data/low density) have not been observed, but complete the experimental design and allow examination of other ecological circumstances.

The results for the peak of lactation are summarized in Table 28. The negative signs on the balance values indicate demand on the female's reserves. The values may be related to requirements by noting that the grand mean of EBF (-53.883) is about 6 percent of the female's energy requirement and the grand mean of PBF (-26.577) is about 4 percent of the protein requirement. Analyses of variance (Table 29) show that density, diet, and their interaction had no significant effect (p > 0.05) on either energy or protein balance at peak
Table 28. Mean simulated energy balance (EBF, kcal/indiv./day) and protein balance (PBF, g CP/indiv./day) of female jackrabbits at peak lactation under high and low density and dietary inputs. Means were generated from 40 simulations with the jackrabbit experimental model run with parameters chosen randomly.

<table>
<thead>
<tr>
<th>Dietary input</th>
<th>Density conditions</th>
<th>Dietary treatment (row) means</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Low</td>
<td>High</td>
</tr>
<tr>
<td></td>
<td>EBF</td>
<td>PBF</td>
</tr>
<tr>
<td>Data from present study</td>
<td>-70.301</td>
<td>-34.492</td>
</tr>
<tr>
<td>Data from Westoby (1973)</td>
<td>-44.711</td>
<td>-25.023</td>
</tr>
<tr>
<td>Density treatment (column) means</td>
<td>-57.506</td>
<td>-29.758</td>
</tr>
<tr>
<td>Grand means</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 29. Analysis of variance of simulated energy balance (EBF, kcal/indiv./day) and protein balance (PBF, g CP/indiv./day) of female jackrabbits at the peak of lactation under high and low density conditions and dietary inputs.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>EBF MS</th>
<th>EBF F</th>
<th>PBF MS</th>
<th>PBF F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>39</td>
<td>823.661</td>
<td></td>
<td>225.136</td>
<td></td>
</tr>
<tr>
<td>Density</td>
<td>1</td>
<td>525.190</td>
<td>0.668</td>
<td>404.687</td>
<td>1.876</td>
</tr>
<tr>
<td>Diet</td>
<td>1</td>
<td>1577.285</td>
<td>2.005</td>
<td>35.816</td>
<td>0.166</td>
</tr>
<tr>
<td>Den. x diet</td>
<td>1</td>
<td>1698.070</td>
<td>2.158</td>
<td>574.034</td>
<td>2.661</td>
</tr>
<tr>
<td>Error</td>
<td>36</td>
<td>786.728</td>
<td></td>
<td>215.717</td>
<td></td>
</tr>
</tbody>
</table>
lactation. This indicates that there is as much variation within the system as there is in dietary differences or population density. Therefore, we fail to reject H(5); simulated nutritional balance of lactating females is not significantly altered at high densities.

Simulated nutritional balance for female rabbits immediately prior to the breeding season (Table 30) are generally lower than those at peak of lactation (Table 28), indicating that the females are not as nutritionally stressed after the overwinter period. In the experimental situation representing the low density regime (1976 inputs) both energy and protein balances were positive, but for high density (1972), they were both negative. The effect of density treatment on energy balance of females entering the breeding season was significant (p < 0.05) and the effect on protein balance was highly significant (p < 0.001). Diet and the interaction of dietary input and density were not significant (Table 31).

To explain these results, consider that under the low density inputs the average conception date was Julian date 18 compared to a conception date of Julian date 27 in the high density run. Since vegetation quality deteriorated more toward the late winter, it is surprising that no interaction with dietary input was present. In 1976, more than half the observed diet was dominant shrubs with energy content averaging 4.665 kcal/g. However, in 1972, half of the diet was Halogeton, which has an energy content of only 3.000 kcal/g. The explanation of the differences probably lies in the differences in the average size of the first litter. In the high density data set the first litter averaged two young per female.
Table 30. Mean simulated energy balance (EBF, kcal/indiv./day) and protein balance (PBF, g CP/indiv./day) of female jackrabbits entering the breeding season under high and low density conditions and dietary inputs. Means were generated from 40 simulations with the jackrabbit experimental model run with parameters chosen randomly.

<table>
<thead>
<tr>
<th>Density conditions</th>
<th>Dietary treatment (row) means</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Low</td>
</tr>
<tr>
<td></td>
<td>EBF</td>
</tr>
<tr>
<td>Dietary inputs</td>
<td></td>
</tr>
<tr>
<td>Data of present study</td>
<td>1.955</td>
</tr>
<tr>
<td>Data of Westoby (1973)</td>
<td>-10.425</td>
</tr>
<tr>
<td>Density treatment (column) means</td>
<td>-4.235&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Grand means</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Signifies significant difference, p ≤ 0.05.

<sup>b</sup> Signifies significant difference, p ≤ 0.001.
Table 31. Analysis of variance of simulated energy balance (EBF, kcal/indiv./day) and protein balance (PBF, g CP/indiv./day) of female jackrabbits just entering the breeding season under high and low density and diet.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>EBF</th>
<th>PBF</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>F</td>
</tr>
<tr>
<td>Total</td>
<td>39</td>
<td>230.194</td>
<td></td>
</tr>
<tr>
<td>Density</td>
<td>1</td>
<td>1044.893</td>
<td>5.265&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>Diet</td>
<td>1</td>
<td>264.710</td>
<td>1.334</td>
</tr>
<tr>
<td>Den. x diet</td>
<td>1</td>
<td>523.452</td>
<td>2.638</td>
</tr>
<tr>
<td>Error</td>
<td>36</td>
<td>198.459</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Signifies significant effect, p ≤ 0.05.

<sup>b</sup> Signifies significant effect, p ≤ 0.001.
This litter size is larger than average first litter size under high density conditions. Since energy and protein balances were sampled immediately prior to the first parturition, they reflect the difference in carrying a larger litter to term under the poor nutritional conditions of late winter. Average simulated nutritional deficiencies amount to less than 10 percent of the females' requirements. In both experiments females were able to compensate for the deficiency and gain weight, although more slowly in the high density year. What is more important to the population is that the simulation experiments at peak lactation indicate that the female was able to recover productivity later in the breeding season.

These nutritional balance results reject H(6): that females entering the breeding season under high density conditions do not have significantly altered energy and protein balances. This rejection must be interpreted in the light of the small absolute value of nutritional deficiency, the "recovery" of the female by the middle of the breeding season, and the fact that the early breeding date and large litter size are not characteristic of high densities in general.

Consumption functional response

The final hypothesis tested with model experiments was the effect on population dynamics of the functional response to changing available forage. Since Noy-Meir (1975) noted that the stability of simple plant-herbivore systems was affected by this response, this hypothesis might be a connecting link between populations and
available forage. Four functional forms were considered (see Figure 6). Data sets were diet and density initial conditions corresponding to high density by Westoby (1973). As noted in Model Development, parameters were difficult to estimate for these functions because of a lack of a data base specific to jackrabbits. The important point seems to be at what value of available biomass does the function reach (or approach) the value of CMAX and how abruptly does it do so. The functions (see Appendix A for parameter values) reached 90 percent of the value of CMAX in the range of 180 to 800 kg/ha of available forage depending on parameter estimates.

For the control run (Table 32), there was no functional response and the consumption function is constantly CMAX. There is virtually no difference in the fall population density of adults or subadults for any of the functional responses (Table 32). Energy and protein balances were virtually unaffected by any of the treatments.

This result is expected because forage availability under the high density conditions ranged from 1100 to 1900 kg/ha. Under these forage conditions each of the functions would be near CMAX so there is virtually no difference between the control and any of the different form treatments. Since nutritional dynamics are insensitive to maximum consumption (Table 25) and to functional response, nutrition and population dynamic responses will not be affected by forage availability over ranges that have been observed.

This simulation test fails to reject H(7); that population density will not be sensitive to the jackrabbits functional response
Table 32. Simulated density and nutritional response to various forms of consumption functional response. Consumption functions parameterized and tested were: A - control (function is constant = CMAX); B - ramp, C - Michaelis-Menton; D - Von Bertalanffy; E - logistic (see Figure 9).

<table>
<thead>
<tr>
<th>Output variable</th>
<th>Consumption function form</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
</tr>
<tr>
<td>Fall census TAD (indiv./ha)</td>
<td>0.147</td>
</tr>
<tr>
<td>Fall census TSUB (indiv./ha)</td>
<td>0.235</td>
</tr>
<tr>
<td>Peak lactation EBF (kcal/indiv./day)</td>
<td>-42.632</td>
</tr>
<tr>
<td>Peak lactation PBF (g CP/indiv./day)</td>
<td>-25.200</td>
</tr>
</tbody>
</table>
to available vegetation. However, the derivation of parameters for the functional forms for jackrabbit response was somewhat arbitrary. Such functional responses should be based on changes in behavior documented in the field. The failure to reject may therefore be a failure of the test. The result does support the conclusion that jackrabbit populations in Curlew Valley are not limited by available forage, even at high population densities.

Table 33 is a summary of the experimental results of the hypothesis tests of this study. The interpretation and implications of these results for food limitation in jackrabbit population follows in the DISCUSSION.
Table 33. A summary of the study hypotheses and the results of the associated experiments.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Result</th>
</tr>
</thead>
<tbody>
<tr>
<td>H(1): Dietary composition unaffected by changes in availability above 10 kg/ha.</td>
<td>Rejected; significant correlation between percent in diet and availability for palatable species.</td>
</tr>
<tr>
<td>H(2): Jackrabbits do not require more forage than is available at high population densities.</td>
<td>Fail to reject; simulated requirements constitute a small fraction of available herbage.</td>
</tr>
<tr>
<td>H(3): Average dietary composition is not significantly different in high and low density periods.</td>
<td>Fail to reject; no significant differences between either diet composition or preference.</td>
</tr>
<tr>
<td>H(4): Average dietary composition is not significantly different between breeding males and females.</td>
<td>Fail to reject; no significant differences between either diet composition or preference.</td>
</tr>
<tr>
<td>H(5): Nutritional balance of lactating females is not significantly altered at high density.</td>
<td>Fail to reject; no significant differences in simulated energy or protein balances.</td>
</tr>
<tr>
<td>H(6): Nutritional balance of females entering the breeding season is not significantly altered at high density.</td>
<td>Rejected; significant effects on simulated energy and protein balance caused by density but not dietary input.</td>
</tr>
<tr>
<td>H(7): At high density, population dynamics are not sensitive to consumption functional response.</td>
<td>No test; no significant change in simulated consumption and no effect on simulated population density.</td>
</tr>
</tbody>
</table>
DISCUSSION

The following discussion attempts; (1) to answer some general questions raised by this study about plant-herbivore interactions, and (2) to specifically interpret the results of the field and simulation studies in relation to jackrabbit population processes.

Plant-Herbivore Interactions

Available forage

The problem of defining "available forage" for a herbivore is difficult but it is central to understanding plant and herbivore interactions. Some studies considered above-ground plant material as "available" (Harper 1969). This approach may grossly overestimate availability where poorly-digested, woody species are concerned. Some other studies have eliminated these woody parts of plants from estimates of available biomass, based on their observations of plant parts that are most often taken. In the present study, woody parts larger than a pencil were not considered available. However, this definition may be too conservative, failing to recognize the behavioral responses of the animals when they are nutritionally stressed. Jackrabbits occasionally chew the bark off woody portions and actually ingest some proportion of woody material. Limiting availability to above-ground is also questionable since jackrabbits sometimes dig below ground to get roots.
Gardarsson and Moss (1970) and Pyke et al. (1977) emphasized the role of selectivity in defining what is available, including selectivity of individual plants and plant parts. Such selection may be made on the basis of a variety of proximal cues like smell, color or taste (Arnold 1964) or nutrient content through long-delay learning (Westoby 1974).

The forage spatial distribution may be important in determining availability for a population of herbivores. Use of habitats may be largely determined by cover characteristics (Moen 1973), and available forage may be only that within an individual's habitat. Habitat relationships vary seasonally with changing cover requirements. Highly palatable forage may be neglected because it occurs in areas of low cover value. For example, jackrabbits seldom venture more than 300 m into crested wheatgrass seedings (Westoby 1973) even though forage availability and quality is high.

The solution to defining availability may be to include all of the plant material, including below-ground parts. Studies of interactions between plants and herbivores could then be cost-benefit analyses. That is, what does it "cost" an animal in terms of energy expenditure, exposure to predators, etc. to select and utilize a forage type. This "cost" must be balanced by the "benefit" that the animal derives in nutrients for physiological functions.
Diet selection

For a large generalist herbivore, like jackrabbits, digestion time and efficiency are the limiting factors in diet selection, not search or pursuit time (Westoby 1974, Janis 1976, Pyke et al. 1977). Therefore consumption should be poorly correlated with availability. This prediction held for forage types of low preference (Atriplex confertifolia, Halogoton) (Figures 10 and 13), but was rejected for preferred species like Atriplex falcata, grasses and Bassia (Figures 11, 12 and 14). Of these forage types, grasses are considered the most nutritious and easily digested, and theory predicts greater specialization on the species providing greatest benefit regardless of the abundance of other species (Pyke et al. 1977). Grasses were readily available to all jackrabbits in the vicinity of the crested wheatgrass seeding, yet direct responses to the availability of Atriplex falcata and Bassia were evident. Either these forage types are all equivalent in terms of preference, or jackrabbits are exhibiting partial preferences. Westoby (1973) found evidence that Halogoton was selected during the last jackrabbit population high in Curlew Valley. Evidence from the present study showed that in the short term these generalist herbivores respond to the availability of forage.

No existing theory of diet selection is adequate for predicting diets when nutrient constraints, random variations in food abundances or interactions of plant toxins apply (Pyke et al. 1977). Westoby (1978) suggested a series of situations which would encourage variation
in diet selection: (1) a saving in search costs can be made by taking several foods, (2) benefit to the animal changes because of changes in relative abundance or nutrient content, (3) diet selection includes a sampling component because of changes in abundance, and (4) different foods are important sources of different nutrients. Each of these will be examined in light of the evidence from jackrabbits.

Search costs for jackrabbits feeding in the vicinity of wheatgrass seedings or pure stands of *Atriplex falcata* involve risk to predation. Despite the presence of these highly available, nutritious forages, jackrabbit diets seldom contain more than 50 percent of these forages. High risk to predation should result in more diverse diets (Westoby 1978). Diets may be less varied when the habitat is coarse-grained with respect to the herbivore's home range (Westoby 1978). This is the case for jackrabbits in winter habitats, when the diet is predominantly abundant, poor quality, dominant shrubs because of the high energy expenditure of searching for higher quality forage.

When there are changes in relative abundance, patchiness or changes in nutrient content, dietary variety is predicted (Westoby 1974, Pyke et al. 1977). Even when foods are well interspersed, there will be a high variation between species in the diet, taken in a single feeding period (Westoby 1978). The high variation in the observed diets of jackrabbits taken in the same feeding habitats supports this contention.
It is difficult to collect data relevant to Westoby's (1978) last two contentions. It is certainly true that the quality of a herbivore's diet is constantly changing (Cook and Harris 1968) and that herbivores cannot always detect nutrient quality from proximal cues (Arnold 1964). It is logical, therefore, that sampling should play an important role in providing an adequate input of important nutrients in the diet at any time. Whether this sampling is a form of nutritional wisdom mediated by long-delay learning, as Westoby (1974) has suggested, is highly questionable. Zahorik and Houpt (1977), after reviewing the evidence for nutritional wisdom in large herbivores, concluded that innate preferences for a variety of food cues loosely associated with nutritional value probably account for most of the so-called nutritional wisdom in large generalist herbivores. Thus, the evidence to date offers only a very general explanation of the herbivores' successes and failures in selecting dietary components.

Jackrabbit Population Processes

Dietary composition and preference

The composition of diets of black-tailed jackrabbits in Curlew Valley are similar to the reported diets throughout the range of the species. Jackrabbits browse woody vegetation in winter, utilize grasses mostly in spring, and take a variety of forage, especially grasses and forbs, in summer. Judging from the variety of species in stomach contents, jackrabbits will eat small amounts of almost any vegetation.
Plant species that are rare in the habitat (i.e., *Sphaeralcea* sp., *Penstemon* spp.) often occurred in the jackrabbit stomachs. Whether the jackrabbits actually searched for these plants is open to question since Currie and Goodwin (1966) noted that jackrabbits take a large proportion of the individual plant when they encounter such a preferred plant during their feeding period. Rare and preferred plants might, therefore, be under severe browsing pressure from jackrabbits as Westoby (1974) suggested.

In contrast to Westoby's (1973) study in Curlew Valley, *Halogeton* and *Kochia* were not important in the jackrabbit diets in 1976. The reported importance of *Halogeton* is difficult to understand since it is not particularly exceptional in nutrient content (with the exception of water content). The difference between the two studies may be related to the abundance of other forbs (e.g., *Bassia*) during 1976.

The unimportance of *Kochia* in diets observed in the present study is surprising however. Westoby (1973) reported that *Kochia* was a highly preferred species and this study indicates that it is more abundant now than during 1971-1972. The direct response to availability discussed earlier predicts that *Kochia* should have been more common in jackrabbit diets. An ecologically similar species, *Atriplex falcata*, was important in the diet in 1976. This difference may be a result of sampling and the differences in collection locations in the two studies. Rabbits were more frequently collected in the vicinity of *Atriplex falcata* stands in the present study than during Westoby's (1973) study.
From the evidence presented it seems that (1) jackrabbits at some time try nearly all species of plants present and individual's stomach contents vary considerably, and (2) there were no significant differences between the diets selected by jackrabbits during high and low density periods.

**Forage requirements and vegetation utilization**

From average consumption rates and population density, Westoby (1973) calculated that peak jackrabbit populations could consume about 37 kg/ha/yr in most areas. Model simulations predicted 25-33 kg/ha/yr for a peak year. Simulations showed that, even at high densities, jackrabbits consume only a small fraction (less than 1 percent) of the available standing crop of forage.

In contrast, jackrabbits at low density in 1976 removed an average of 3.71 percent of the standing crop of Kochia and as much as 6.45 percent during winter. A nine-fold increase in jackrabbit density would project to removal of 33.39 and 58.05 percent of the Kochia year-round and in winter respectively. Exclosure studies and valley-wide estimates showed that only a small percentage (average 8 percent) of the plants were browsed. This figure could be projected to 72 percent of Kochia plants browsed at peak jackrabbit density. These calculations suggest that such a palatable species might be impacted during jackrabbit peaks. Westoby (1973)
reached a similar conclusion about the utilization of Kochia.

The above assumes that there is a linear relationship between Kochia utilization and jackrabbit density. However, the diet data show variable responses to changes in relative abundance and partial preferences. It is unlikely that the linearity assumption is useful. If herbivory is largely of an episodic nature, as Shinn et al. (1975) suggested, the overall impact on Kochia may be minimal even at high densities of jackrabbits. Rice and Westoby (1978) found no consistent effects on density or cover of plant species in these salt desert communities protected from jackrabbits. In one case where response of Kochia could be documented, protection from sheep and jackrabbits had no effect on density or coverage. Winterfat (Ceratoides lanata), a similar suffrutescent, increased in cover but not density when protected from herbivory. Apparently even peak jackrabbit density does not affect the dynamics of these suffrutescents.

**Nutritional/physiological system and the population interface**

The simulation studies emphasized interactions between the nutritional/physiological system and population dynamics. The model mechanisms maintain nutritional balance through increased intake, utilization of body stores and reduction of energy and protein expenditures. Reduction of expenditures may be particularly important in the interaction of the individual's system and the population response, if these reductions affect gestation or lactation expenditures. Severe reductions in gestation or lactation expenditures
may have direct demographic consequences in the form of prenatal or neonatal mortality. Gestation expenditures are generally not great until the latter third of gestation and even then constitute no more than a 30 percent increase in energy requirements above maintenance level (Kaczmarski 1966, Randolph et al. 1977). In contrast, increases in lactation requirements are great, and may be an important stress for adult females. Simulated energy and protein demand, and forage intake were as much as 300 percent greater in lactating female jackrabbits than in non-reproducing females. Large litters (> 5) placed especially high demands on the females. These results agree with the simulations of Heasley (1977) and the empirical studies of Kaczmarski (1966) and Randolph et al. (1977).

Although jackrabbits compensate for increased nutritional demands through increased intake, such compensation may be incomplete if vegetation is of poor quality or if availability is restricted. The result is that production of fetuses and milk may be restricted. Milk production may be particularly influenced, especially at the peak of lactation when demand from the young is the greatest. Young may be allowed a shorter nursing time each day and weaning may occur at an earlier age, forcing the young to take green forage at an earlier age. Cameron (1973) and Randolph et al. (1977) showed that there is an inverse linear relationship between average growth rate of young and litter size in some mammals. Food shortage to the mother directly influences the growth rate of young mice (Millar 1975, Heasley 1977). If milk production during lactation for large litters of jackrabbits is insufficient, then
it is reasonable to expect poorer growth and lower body weights as observed in other species. These potential changes, particularly those associated with maternal care, deserve additional attention from the field biologist.

Poor maternal nutrition and growth of young have been implicated many times as a cause of early mortality. Loose correlations are found between poor maternal nutrition, growth of young and subsequent survival in deer (Klein 1970) and between weight gain of young and survival in snowshoe hares (Keith and Windberg 1978). The mechanisms involved are poorly understood. Millar (1975) showed food shortage for breeding populations was related to mortality of nesting Peromyscus. Cameron (1973) found that survival was lower in large litters of woodrats. Undernourished or small young may be susceptible to predation or changing weather conditions (Cameron 1973). The period of weaning may be especially critical, as young animals try to adapt to a new diet of green forage. If weaning is earlier than normal, digestive disorders often occur (Maynard and Loosli 1969), and these may result in mortality. Similar relationships may be found among growth, body weights, and survival of young jackrabbits.

In many cases maternal survival is unaffected by the stresses of reproduction (Randolph et al. 1977). The maternal response is generally to restrict production, thus transferring the effects of shortage to the offspring. Cameron (1973), however, did attribute some maternal deaths to weaning of unusually large litters.

An interesting result of the simulation studies is that, in general, protein balance was less severely affected than energy balance
under the stresses of high physiological demand. Jackrabbits seem to be most limited by the amount (i.e., energy) of forage that they can process. In this sense, jackrabbits are like other large generalist herbivores (Westoby 1974). Their "strategy" seems to be to process forage as fast as possible, rather than to increase assimilation efficiency (Janis 1976). Under these circumstances, assuming even minimal assimilation of dietary protein, protein balance seems to be little of a problem.

Sensitivity tests of the nutrition submodel showed it to be insensitive to errors in parameters. Stochastic runs showed that system output was reasonably well-behaved, even in the face of substantial parameter error. Heasley (1977) and Anway (1978) experienced similar success with nutritional/physiological models of mammalian systems. These results can be attributed to two conditions: (1) the relatively well-known nutritional/physiological mechanisms, and (2) the data base which provides accurate and precise estimates for parameters. This situation is in contrast to modeling other levels in ecological studies (e.g., the level of the population) where mechanisms may be unknown and parameters derived from correlation.

Food limitation hypotheses

Examining the contention that the above nutritional/physiological interactions could be related to the density of the population, and that forage resources may be limiting during periods of high density, was the main objective of this study. The empirical studies confirmed that jackrabbits are selective herbivores, but showed that
they respond to availability of palatable species. However, dietary composition, on a species basis, was not significantly different between densities or sexes. These tests showed that differences in diet are not caused by the changes in relative availability of forage that have occurred in Curlew Valley. Simulated nutrition was unaffected by diet or population density during lactation. Density treatment did affect early breeding season energy and protein balance, but this effect did not persist into lactation period. Jackrabbits, even at high densities, do not require more forage than is available to support their populations.

These conclusions lead to the rejection of the contention that jackrabbit nutrition is altered at high density by food limitation. Differences in mortality patterns, which initiate population declines in the Curlew Valley, are apparently unrelated to differences in diet and nutrition.

Stoddart (1975) identified two factors, a density related factor, and an unknown factor, that were correlated with the change of birth-October mortality of juveniles. When the present study was initiated, it appeared that nutrition might be implicated in the density related factor. The simulation tests show that this connection is unlikely.

More recent analysis by Stoddart (1977) showed that these density related factors are unnecessary to explain observed changes in jackrabbit mortality, and that coyote predation alone suffices. He concluded "with the observed functional and numerical response of the
coyote population to jackrabbit density and with jackrabbit behavioral changes the general trend of the observed jackrabbit 'cycle' can be accounted for by coyote predation alone" (Stoddart 1977:31).

There is, however, considerable variation in mortality from unknown factors plus experimental error in Stoddart's studies. The nutritional/physiological system may contribute to this variation. An exceptionally harsh overwinter period, late initiation of plant growth, or large litters may result in nutritional stress and increase juvenile or adult mortality. Nutritional stress may contribute to mortality, but this study shows that this contribution is unrelated to population density.

The above discussion contrasts with conclusions of Keith (1974) and Keith and Windberg (1978) regarding the causes of population cycles of snowshoe hares. Their conceptual model hypothesizes a hare-vegetation interaction at peak densities, which causes reduced adult weight and slower juvenile growth rate, which are related to subsequent survival. Two important components of their ideas are: (1) that the browsing hares significantly reduce their overwinter food supply during population highs, and that the resulting (2) dietary differences cause a nutritional deficiency which affects hare demography. Both model simulations and field data of the present study refute component (1) for the Curlew Valley jackrabbits. Simulations of jackrabbit nutrition and population dynamics also refute component (2) for these populations.

Population cycles of rodents in field studies (Pitelka 1957, 1973) have been characterized by an animal-food resource interaction.
Key relationships in these interactions seem to be impact on production potential of the vegetation and a close link between diet selection and nutritional balance. Heasley (1977) showed that the energy resource patterns (frequency and amplitude) significantly influenced the simulated dynamics of rodent populations. Unfortunately, there is often a scarcity of qualitative and quantitative data on small rodent nutrition (Batzli and Pitelka 1971, Heasley 1977). In addition, the critical rodent-vegetation interaction is apparently not always characteristic of population highs everywhere (Krebs 1964).

There is evidence that ungulate eruptions and declines are also caused by discrepancies between populations and their forage (Caughley 1970, Sinclair 1974). Nutrition is affected, fat reserves depleted and mortality increased when ungulate populations exceed their food resources.

The above types of fluctuating populations seem to have common elements and similar demographic patterns of birth, mortality and movements. Watson (1977) emphasized that red grouse studies illustrate characteristics consistent with almost every major hypothesis of what causes population fluctuations. Perhaps as Keith (1974) concludes, the patterns of immediate population change are part of a "General Demographic Syndrome" in response to a variety of intra-specific and environmental stressors. Populations, even of the same species, show patterns of changes in size that are either largely density-dependent or largely density-independent (Ehrlich et al. 1975). Changes in behavior of herbivores, predation, and perhaps also in their physiology and genetic makeup help to integrate the population
with the available food resources. The key questions remaining involve the distribution of the herbivores in relation to available forage, their foraging behavior, assimilation efficiency, and the cost-benefit of obtaining nutrients. The generality of conclusions can only be tested by examining additional, carefully selected species, and by long-term, in-depth studies of population ecology.
SUMMARY AND CONCLUSIONS

In summary, this study consisted of field experiments on dietary composition, vegetation utilization, and a simulation model of nutrition and population dynamics. These methods were used to examine the impact of forage limitation on jackrabbit population dynamics in Curlew Valley, Utah. Seven hypotheses were developed and examined that are consequences of food limitation. Subject to the assumptions of the field studies and the model simulations, conclusions which may be drawn from the analyses are:

1) In the short term, occurrence of preferred plant species in the diets of jackrabbits is directly related to the available plant biomass.

2) Jackrabbits do not require more forage than is available to them at high population densities. Jackrabbits consume less than 1 percent of all forage available.

3) Dietary composition and preference is highly variable and average dietary composition is not significantly influenced by density.

4) Average dietary composition is not significantly different between breeding males and females.

5) Simulated nutritional balance of lactating females is not significantly altered at high densities. Neither density nor diet affects energy or protein balance during lactation.
6) Simulated nutritional balance of females entering the breeding season is unaffected by observed diet variations but may be affected by early breeding or large litter size. Early breeding and large litter size are not necessarily related to density.

7) Availability is never low enough to substantially reduce intake of jackrabbits.

Generally, individual nutritional response and its interaction with food does not cause significant change in population mortality rates. Nutritional limitations could contribute to mortality, particularly during lactation or winter periods, but these effects are independent of population density.
LITERATURE CITED


APPENDICES
Appendix A

Variable and Parameter Dictionary and

Input Values Plus Sources
Variable Dictionary

ABF - activity multiplier, breeding females (dimensionless)
ABM - activity multiplier, breeding males (dimensionless)
AFF - activity multiplier, females (dimensionless)
AFM - activity multiplier, males (dimensionless)
AFMORT - adult female mortality rate (density/density*day)
AFNAT - nutrition dependent adult female natural mortality rate (density/density*day)
AGE - fall age ratio of adults: total population (dimensionless)
AHI - average heat increment fraction (dimensionless)
ALITS - average litter size at time T (young/female)
AMMORT - adult male mortality rate (density/density*day)
AMNAT - nutrition dependent adult male natural mortality rate (density/density*day)
AYA - activity increment of young, before TA1 (dimensionless)
AYB - activity increment at birth (dimensionless)
AYC - rate of change of activity increment (1/day)
AYD - activity increment of young and juveniles (dimensionless)
BAL - energy balance point (kcal/indiv.*day)
BH - weight reduction parameter (kg/indiv.)
BHP - basal heat production (kcal/indiv.*day)
BPF - body protein fraction (g CP/kg)
BRATE - male body weight change (kg/indiv.*day)
C1 - potential growth rate of fetus, T < 12 (kg/indiv.*day)
C2 - potential growth rate of fetus, 12 ≤ T < 24, (kcal/indiv.*day)
C3 - potential growth rate of fetus, 25 ≤ T ≤ GEST (kcal/indiv.*day)
CASMN - length of summer period (days)
CASMNT - instantaneous adult natural mortality rate in summer (Apr-Oct) (density/density*day)
CASMPD - instantaneous adult predation mortality rate in summer (Apr-Oct) (density/density*day)
CAT - fat catabolism efficiency (dimensionless)
CFPRD - population predation mortality rate in winter (density/density*day)
CJ - potential juvenile growth parameter (kg/kg/day)
CJMN - length of birth to Oct period (days)
CJMNAT - juvenile natural mortality rate (birth-Oct) (density/density*day)
CJMPRD - juvenile predation mortality rate (birth-Oct) (density/density*day)
CMFN - g crude protein lost per kg forage eaten (g/kg)
CNG - nitrogen fraction of gain (dimensionless)
CORP - fraction of nitrogen requirement from corprophagy (dimensionless)
CP - crude protein content of forage (percent)
CPDIET - average crude protein of diet (percent)
CPDIG - crude protein digestibility coefficient (dimensionless)
CPIN - crude protein intake (g/indiv.*day)
CWMN - length of winter period (days)
CWMNAT - population natural mortality rate in winter (density/density *day)
CWMPRD - population predation mortality rate in winter (density/density *day)
CY - potential young growth rate (kg/day)
DADF - density of adult female (no./ha)
DADM - density of adult males (no./ha)
DBFLO - density flow of adult males (no./ha*day)
DDFLO - density flow of adult females (no./ha*day)
DERL - energy requirement for lactation (kcal/indiv.*day)
DFFLO - density flow of fetuses (no./ha*day)
DFT - density of fetuses (no./ha)
DIET - proportion in diet of forage type (dimensionless)
DIG - energy digestibility coefficient (dimensionless)
DIGMCP - milk protein digestibility coefficient (dimensionless)
DJFLO - density flow of juveniles (no./ha*day)
DJUV - density of juveniles (no./ha)
DMP - daily milk production (g/day)
DRATE - female body weight change rate (kg/indiv.*day)
DRY - dry fraction of body weight (dimensionless)
DSUB - subadult density (no./ha)
DT - time step (days)
DYFLO - density flow of young (no./ha*day)
DYNG - density of young (no./ha)
E1 - fraction of ELAB from gestation (dimensionless)
E2 - fraction of ELAB from lactation (dimensionless)
EDU - energy deficiency ratio (dimensionless)
EFAT - energy content of fat (kcal/kg)
ELAB - labile energy (kcal/day)
EMLKCN - metabolizable energy in milk consumed (kcal/indiv.*day)
EPRO - energy content of protein (kcal/kg)
ERYF - energy reduction factor of growth of young (dimensionless)
EUN - endogenous urinary nitrogen loss (g/indiv.*day)
FBSPE - female breeding season energy balance (kg/indiv.*day)
FDIF - food intake increment, females (dimensionless)
FDIM - food intake increment, males (dimensionless)
FETRED - fetal growth reduction factor (dimensionless)
FMN - fraction milk nitrogen (dimensionless)
FPOP - fall population density (no./ha)
FRAJ - fraction of juveniles in litter J (dimensionless)
FRATE - fetal body weight change rate (kg/indiv.*day)
FTGER - fraction of TGERT attained (dimensionless)
GAINC - activity increment of energy requirements (dimensionless)
GE - gross energy of forage (kcal/g)
GEDIET - average gross energy of diet (kcal/g)
GEIN - gross energy intake (kcal/indiv.*day)
GEMLK - gross energy in milk (kcal/g)
GER - gestation energy requirement (kcal/day)
GESERF - gestation energy reduction factor (dimensionless)
GESRED - gestation energy reduction (kcal/indiv.*day)
GEST - length of gestation period (days)
GP1 - gestation parameter (kcal/kg1.2)
GP2 - gestation parameter (dimensionless)
GRER - growth energy requirement (kcal/kg)
HP1 - basal metabolism rate constant (kcal/day*kg0.75)
HP2 - metabolism rate constant (dimensionless)
HP3 - lower summer critical temperature (degrees C)
HP6 - upper summer critical temperature (degrees C)
HP9 - lower winter critical temperature (degrees C)
HP12 - upper winter critical temperature (degrees C)
HP4, HP5, HP7, HP8, HP10, HP11, HP13, HP14 - heat production increment parameters
HPINC - heat production increment (dimensionless)
IA - Julian date of autumn population census (day)
IBKII - time after birth when YNG become JUV in population submodel (day)
IBRK - time after birth when YNG growth changes to JUV growth (day)
ICR - time delay in protein shortage effect (day)
IOP - period between litters (days)
IS - Julian date of spring population census (day)
IT1, IT2, IT3 - date of digestibility changes (day)
IT4, IT5 - date of fetal growth rate change (date)
ITT - Julian date of summer temperature acclimation
ITTT - Julian date of winter temperature acclimation
IWK - length of yearly iteration (weeks)
JRATE - juvenile weight change rate (kg/indiv.*day)
LACRED - lactation energy reduction (kcal/indiv.*day)
LAG - Julian date of minimum average temperature (day)
LINC - nitrogen increment of lactation (dimensionless)
LITMAX - maximum number of litters per female (litters/female)
ME - metabolizable energy (kcal/day)
MEDIET - metabolizable energy of diet (kcal/g)
MFN - metabolic fecal nitrogen loss (g/indiv.*day)
MS - month of spring population census
NEMLK - net energy ratio of milk (dimensionless)
NG - nitrogen required for growth (g/indiv.*day)
NL - nitrogen requirement for lactation (g/indiv.*day)
NP - nitrogen requirement for pregnancy (g/indiv.*day)
NYR - year of simulation
NYRSTP - maximum year of simulation
PCAT - protein catabolism efficiency (dimensionless)
PDMP - potential milk production (g/female)
PDU - protein deficiency ratio (dimensionless)
PERM - proportion of males in population (dimensionless)
PINC - nitrogen increment of pregnancy (dimensionless)
PMLKCN - assimilated protein in milk consumed (g/indiv.*day)
PPI - endogenous urinary nitrogen parameter (g N/kg0.75)
PP2 - endogenous urinary nitrogen parameter (dimensionless)
PREG - pregnancy rate of females (dimensionless)
PREMOR - prenatal mortality rate (density/density*day)
PRF - protein reduction factor (dimensionless)
PRYF - protein reduction factor of growth of young (dimensionless)
RATPN - ratio of protein to nitrogen in proteins (dimensionless)
RCFET - fetuses recruited (no./ha)
RCJUV - recruitment of young (no./ha)
RCYNG - young recruited (no./ha)
RD - proportion of energy requirement of young derived from milk (dimensionless)
RDA - proportion of energy requirement of young from milk until weaning begins (dimensionless)
RDB - proportion of energy requirement from milk at birth (dimensionless)
RDC - rate of change of proportion of energy requirement from milk (1/day)
RDD - proportion of energy requirement from milk after weaning (dimensionless)
RMN - reduced fraction milk nitrogen (dimensionless)
RRMN - reduction rate of milk nitrogen fraction (1/day)
SEXR - fraction males at birth (dimensionless)
SF1 - maximum survival multiplier (dimensionless)
SF2 - logistic survival multiplier parameter (dimensionless)
SF3 - logistic survival multiplier parameter (dimensionless)
SNAT - survival rate for one time step (density/density*day)
SPOP - spring population density (no./ha)
ST - total survival rate for a period (density/density)
STOR - proportion of energy requirement from stored reserves (dimensionless)
TA1 - time after parturition when activity increases (day)
TA2 - time before and after conception for change of male activity (days)
TAD - total adult population (no./ha)
TCON - Julian date of conception
TEM1 - mean annual temperature (degrees C)
TEM2 - mean annual temperature amplitude (degrees C)
TEMP - air temperature (degrees C)
TEND - Julian date of end of simulation
TGER - gestation energy requirement (kcal/fetus)
THP - heat production (kcal/indiv.*day)
TISERY - tissue growth energy requirement of young (kcal/indiv.*day)
TLDEL - time of litter growth reduction (day)
TPART - Julian date of parturition
TPJUV - density of juveniles on last day of yearly iteration (no./ha)
TSTART - Julian date of simulation start (day)
TSUB - subadult density (no./ha)
TWN1 - time after parturition that weaning begins (days)
TWN2 - time of end of weaning period (day)
UE - ratio of ME to DE (dimensionless)
VMORT - juvenile mortality rate (density/density*day)
WADF - weight of adult females (kg/indiv.)
The following variables are generic names, each of which appears in the model with an age or sex class designation after it. F - adult female, M - adult male, Y - young, J - juvenile.

- WADM: weight of adult males (kg/indiv.)
- WFET: weight of fetuses (kg/indiv.)
- WJUV: weight of juveniles (kg/indiv.)
- WK: weight of juveniles at age 245 (kg/indiv.)
- WPAR: potential birth weight (kg/indiv.)
- WYNG: weight of young (kg/indiv.)
- YMORT: young mortality rate (density/density*day)
- YNAT: nutrition dependent young natural mortality rate (density/density*day)
- YRATE: young weight change rate (kg/indiv.*day)

- AINC: activity increment (dimensionless)
- DCPR: crude protein requirement (g/indiv.*day)
- DER: existence energy requirement (kcal/indiv.*day)
- EB: energy balance (kcal/indiv.*day)
- FDIN: forage consumed (g/day)
- PB: protein balance (g/indiv.*day)
- RDF: forage required for energy balance (g/day)
- TDER: total daily energy requirement (kcal/indiv.*day)
- RDNR: total daily nitrogen requirement (g/indiv.*day)
Table A.34. Summary of the important parameters of the jackrabbit experimental model, the mean and standard deviation, and the sources from which they were derived.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean</th>
<th>SD</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>ABF (activity breeding female)</td>
<td>1.00</td>
<td>0.05a</td>
<td>Haug (1969), Gessaman (1973)</td>
</tr>
<tr>
<td>ABM (activity breeding male)</td>
<td>1.33</td>
<td>0.165a</td>
<td>Haug (1969), Gessaman (1973)</td>
</tr>
<tr>
<td>AFF (activity factor female)</td>
<td>1.00</td>
<td>0.025a</td>
<td>Gessaman (1973), Costa et al. (1976)</td>
</tr>
<tr>
<td>AFM (activity factor male)</td>
<td>1.10</td>
<td>0.05a</td>
<td>Gessaman (1973), Costa et al. (1976)</td>
</tr>
<tr>
<td>AHI (average heat increment)</td>
<td>0.40</td>
<td>0.063a</td>
<td>Kleiber (1961), Anway (1978)</td>
</tr>
<tr>
<td>AYA (activity change factor)</td>
<td>0.40</td>
<td>0.05</td>
<td>estimated from data of Haug (1969), Gessaman (1973), Moen (1973)</td>
</tr>
<tr>
<td>AYB (activity change factor)</td>
<td>0.214</td>
<td>0.01</td>
<td>Nelson (1970), Gessaman (1973),</td>
</tr>
<tr>
<td>AYC (activity change factor)</td>
<td>0.027</td>
<td>0.005</td>
<td></td>
</tr>
<tr>
<td>AYD (activity change factor)</td>
<td>1.33</td>
<td>0.165</td>
<td></td>
</tr>
<tr>
<td>BAL (energy balance)</td>
<td>0.10</td>
<td>0.05</td>
<td>Brody (1945)</td>
</tr>
<tr>
<td>BH (gestation reduction parameter)</td>
<td>0.0557</td>
<td>0.0114</td>
<td>Hammond (1965)</td>
</tr>
<tr>
<td>BPF (body protein fraction)</td>
<td>0.18</td>
<td>0.02</td>
<td>Maynard and Loosli (1969)</td>
</tr>
<tr>
<td>C1 (fetal growth rate)</td>
<td>0.000012</td>
<td>0.00001</td>
<td>estimated from data of Bookout (1964)</td>
</tr>
<tr>
<td>C2 (fetal growth rate)</td>
<td>0.00047</td>
<td>0.0001</td>
<td></td>
</tr>
<tr>
<td>C3 (fetal growth rate)</td>
<td>0.00581</td>
<td>0.000029</td>
<td></td>
</tr>
<tr>
<td>CASMN (length of summer period)</td>
<td>213.0</td>
<td>21.0</td>
<td>Gross et al. (1974)</td>
</tr>
<tr>
<td>CASMNT (summer natural mortality rate)</td>
<td>0.05</td>
<td>0.005b</td>
<td>Stoddart (1977)</td>
</tr>
<tr>
<td>CASMPD (summer predation mortality rate)</td>
<td>1.512</td>
<td>0.151b</td>
<td>Stoddart (1977)</td>
</tr>
<tr>
<td>CAT (catabolism efficiency)</td>
<td>0.80</td>
<td>0.05</td>
<td>Heasley (1977)</td>
</tr>
<tr>
<td>CDEN (critical density)</td>
<td>0.50</td>
<td>0.20</td>
<td>estimated from Gross et al. (1974)</td>
</tr>
<tr>
<td>CJ (juvenile growth constant)</td>
<td>0.010</td>
<td>0.001</td>
<td>estimated from Haskell and Reynolds (1947)</td>
</tr>
<tr>
<td>CJMN (length of birth to Oct period)</td>
<td>180.0</td>
<td>18.0</td>
<td>Gross et al. (1974)</td>
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</table>
Table A.34. Continued.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean</th>
<th>SD</th>
<th>Source</th>
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<tbody>
<tr>
<td>CJMNAT (juvenile natural mortality rate)</td>
<td>0.48</td>
<td>0.05^b</td>
<td>Stoddart (1977)</td>
</tr>
<tr>
<td>CJMPRD (juvenile predation mortality rate)</td>
<td>0.398</td>
<td>0.04^b</td>
<td>Stoddart (1977)</td>
</tr>
<tr>
<td>CMAX (maximum consumption)</td>
<td>240.0</td>
<td>48.0</td>
<td>estimated from Currie and Goodwin (1966), Westoby (1973)</td>
</tr>
<tr>
<td>CMFN (metabolic fecal nitrogen constant)</td>
<td>5.00</td>
<td>1.13^a</td>
<td>Moen (1973)</td>
</tr>
<tr>
<td>CNG (growth nitrogen constant)</td>
<td>0.025</td>
<td>0.003</td>
<td>Moen (1973)</td>
</tr>
<tr>
<td>CONA (consumption factor)</td>
<td>30.0</td>
<td>30.0</td>
<td>estimated from Noy-Meir (1975)</td>
</tr>
<tr>
<td>CONB (consumption factor)</td>
<td>0.0002</td>
<td>0.0002</td>
<td>estimated from Westoby (1974)</td>
</tr>
<tr>
<td>CONC (consumption factor)</td>
<td>75.618</td>
<td>75.618</td>
<td></td>
</tr>
<tr>
<td>CONL (consumption factor)</td>
<td>9.042</td>
<td>9.042</td>
<td></td>
</tr>
<tr>
<td>CONS (consumption factor)</td>
<td>876.0</td>
<td>876.0</td>
<td></td>
</tr>
<tr>
<td>CONW (consumption factor)</td>
<td>0.274</td>
<td>0.274^a</td>
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</tr>
<tr>
<td>CORP (coprophagy parameter)</td>
<td>0.10</td>
<td>0.025</td>
<td>Moen (1973)</td>
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<tr>
<td>CWMN (length of winter period)</td>
<td>150.0</td>
<td>15.0</td>
<td>Gross et al. (1974)</td>
</tr>
<tr>
<td>CWMNAT (winter natural mortality rate)</td>
<td>0.38</td>
<td>0.038</td>
<td>Stoddart (1977)</td>
</tr>
<tr>
<td>CWMPRD (winter predation mortality rate)</td>
<td>0.980</td>
<td>0.098^b</td>
<td>Stoddart (1977)</td>
</tr>
<tr>
<td>CY (young growth constant)</td>
<td>0.01714</td>
<td>0.00386</td>
<td>estimated from Haskell and Reynolds (1947)</td>
</tr>
<tr>
<td>DIGMCP (digestibility of milk protein)</td>
<td>0.90</td>
<td>0.025</td>
<td>Moen (1973)</td>
</tr>
<tr>
<td>DRY (body dry weight fraction)</td>
<td>0.30</td>
<td>0.06</td>
<td>Altman and Dittmer (1968)</td>
</tr>
<tr>
<td>DT (time step)</td>
<td>1.0</td>
<td></td>
<td>chosen for convenience</td>
</tr>
<tr>
<td>EFAT (energy content of fat)</td>
<td>9300.0</td>
<td>135.0</td>
<td>Maynard and Loosli (1969)</td>
</tr>
<tr>
<td>EPRO (energy content of protein)</td>
<td>5650.0</td>
<td>220.0</td>
<td>Maynard and Loosli (1969)</td>
</tr>
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</table>
Table A.34. Continued.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean</th>
<th>SD</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>FBSPE (female breeding season energy balance)</td>
<td>2.00</td>
<td>1.00</td>
<td>Brody (1945)</td>
</tr>
<tr>
<td>FDIF (food ingestion parameter, females)</td>
<td>0.02</td>
<td>0.002b</td>
<td>personal estimates</td>
</tr>
<tr>
<td>FDIM (food ingestion parameter, males)</td>
<td>0.01</td>
<td>0.001b</td>
<td>personal estimates</td>
</tr>
<tr>
<td>FMN (fraction milk nitrogen)</td>
<td>0.0195</td>
<td>0.002</td>
<td>Altman and Dittmer (1968)</td>
</tr>
<tr>
<td>GAINC (general activity increment)</td>
<td>0.40</td>
<td>0.05</td>
<td>estimated from Crampton and Harris (1969), Moen (1973)</td>
</tr>
<tr>
<td>GEMLK (gross energy of milk)</td>
<td>2.00</td>
<td>0.40</td>
<td>Altman and Dittmer (1968)</td>
</tr>
<tr>
<td>GEST (gestation length)</td>
<td>42.0</td>
<td>2.0</td>
<td>Haskell and Reynolds (1947), Gross et al. (1974)</td>
</tr>
<tr>
<td>GP1 (gestation parameter)</td>
<td>2827.0</td>
<td>200.0</td>
<td>Brody (1945)</td>
</tr>
<tr>
<td>GP2 (gestation parameter)</td>
<td>1.2</td>
<td>0.025</td>
<td>Brody (1945)</td>
</tr>
<tr>
<td>GRER (growth energy requirement)</td>
<td>8193.0</td>
<td>784.0</td>
<td>Holter et al. (1974)</td>
</tr>
<tr>
<td>HP1 (metabolic rate constant)</td>
<td>70.0</td>
<td>1.2</td>
<td>Kleiber (1961)</td>
</tr>
<tr>
<td>HP2 (metabolic rate constant)</td>
<td>0.75</td>
<td>0.005</td>
<td>Kleiber (1961)</td>
</tr>
<tr>
<td>HP3 (lower summer critical temperature)</td>
<td>26.0</td>
<td>1.3</td>
<td>Hinds (1977)</td>
</tr>
<tr>
<td>HP4 (heat increment parameter)</td>
<td>2.15</td>
<td>0.22</td>
<td></td>
</tr>
<tr>
<td>HP5 (heat increment parameter)</td>
<td>0.058</td>
<td>0.007</td>
<td></td>
</tr>
<tr>
<td>HP6 (upper summer critical temperature)</td>
<td>34.0</td>
<td>1.70</td>
<td></td>
</tr>
<tr>
<td>HP7 (heat increment parameter)</td>
<td>0.235</td>
<td>0.200</td>
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</tr>
<tr>
<td>HP8 (heat increment parameter)</td>
<td>0.023</td>
<td>0.005</td>
<td></td>
</tr>
<tr>
<td>HP9 (heat increment parameter)</td>
<td>21.00</td>
<td>1.05</td>
<td></td>
</tr>
<tr>
<td>HP10 (heat increment parameter)</td>
<td>1.63</td>
<td>0.137</td>
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</table>
Table A.34. Continued.

<table>
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<th>Parameter</th>
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<th>Source</th>
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<tr>
<td>HP11 (heat increment parameter)</td>
<td>0.030</td>
<td>0.004</td>
<td>Hinds (1977)</td>
</tr>
<tr>
<td>HP12 (upper summer critical temperature)</td>
<td>28.00</td>
<td>1.40</td>
<td></td>
</tr>
<tr>
<td>HP13 (heat increment parameter)</td>
<td>0.588</td>
<td>0.133</td>
<td></td>
</tr>
<tr>
<td>HP14 (heat increment parameter)</td>
<td>0.015</td>
<td>0.006</td>
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</tr>
<tr>
<td>IBKII (young behavior age)</td>
<td>40.0</td>
<td>10.0</td>
<td>personal estimate</td>
</tr>
<tr>
<td>IBRK (young/nuvenile growth break point)</td>
<td>70.0</td>
<td>7.0b</td>
<td>estimated from Haskell and Reynolds (1947)</td>
</tr>
<tr>
<td>ICR (delay in protein shortage effect)</td>
<td>7.0</td>
<td>3.0</td>
<td>Brody (1945)</td>
</tr>
<tr>
<td>IOP (length of period between litters)</td>
<td>2.0</td>
<td>1.0</td>
<td>Stoddart (1972)</td>
</tr>
<tr>
<td>IT4 (fetal growth break point)</td>
<td>12.0</td>
<td>2.0</td>
<td>estimated from Bookout (1964)</td>
</tr>
<tr>
<td>IT5 (fetal growth break point)</td>
<td>24.0</td>
<td>2.0</td>
<td></td>
</tr>
<tr>
<td>ITT (date of summer temperature acclimation)</td>
<td>150.0</td>
<td>21.0</td>
<td>Hinds (1964)</td>
</tr>
<tr>
<td>ITTT (date of winter temperature acclimation)</td>
<td>290.0</td>
<td>21.0</td>
<td></td>
</tr>
<tr>
<td>LAG (date of coldest average temperature)</td>
<td>15.0</td>
<td>15.0a</td>
<td>Balph et al. (1974)</td>
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<tr>
<td>LINC (lactation protein increment)</td>
<td>1.30</td>
<td>0.10a</td>
<td>Moen (1973)</td>
</tr>
<tr>
<td>NEMLK (net energy efficiency of milk)</td>
<td>0.875</td>
<td>0.036a</td>
<td>Moen (1973)</td>
</tr>
<tr>
<td>PCAT (catabolism efficiency of protein)</td>
<td>0.70</td>
<td>0.05a</td>
<td>Heasley (1977)</td>
</tr>
<tr>
<td>PINC (pregnancy protein increment)</td>
<td>1.20</td>
<td>0.05a</td>
<td>Moen (1973)</td>
</tr>
<tr>
<td>PP1 (endogenous urinary nitrogen parameter)</td>
<td>0.146</td>
<td>0.028</td>
<td>Moen (1973)</td>
</tr>
<tr>
<td>PP2 (endogenous urinary nitrogen parameter)</td>
<td>0.75</td>
<td>0.005</td>
<td>Moen (1973)</td>
</tr>
</tbody>
</table>
Table A.34. Continued.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Mean</th>
<th>SD</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>PREMOR (prenatal mortality rate)</td>
<td>0.0025</td>
<td>0.0025</td>
<td>Stoddart (1972)</td>
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<tr>
<td>RATPN (ratio of protein to nitrogen)</td>
<td>6.25</td>
<td>0.20</td>
<td>Kleiber (1961)</td>
</tr>
<tr>
<td>RDA (weaning parameter)</td>
<td>1.000</td>
<td>0.001a</td>
<td></td>
</tr>
<tr>
<td>RDB (weaning parameter)</td>
<td>1.54</td>
<td>0.01a</td>
<td>estimated from Haskell and Reynolds (1947)</td>
</tr>
<tr>
<td>RDC (weaning parameter)</td>
<td>0.077</td>
<td>0.001a</td>
<td></td>
</tr>
<tr>
<td>RRMN (milk nitrogen reduction factor)</td>
<td>0.95</td>
<td>0.025a</td>
<td>Mueller and Sadleir (1977)</td>
</tr>
<tr>
<td>SEXR (sex ratio at birth)</td>
<td>0.50</td>
<td>0.05a</td>
<td>Stoddart (1972)</td>
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<tr>
<td>SF1 (survival multiplier parameter)</td>
<td>1.05</td>
<td>0.105</td>
<td>personal estimates</td>
</tr>
<tr>
<td>SF2 (survival multiplier parameter)</td>
<td>30.0</td>
<td>3.0</td>
<td>personal estimates</td>
</tr>
<tr>
<td>SF3 (survival multiplier parameter)</td>
<td>10.0</td>
<td>1.0</td>
<td>personal estimates</td>
</tr>
<tr>
<td>STOR (proportion of energy requirements</td>
<td>0.15</td>
<td>0.025</td>
<td>Heasley (1977)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TAI (age of activity increase)</td>
<td>7.0</td>
<td>2.0</td>
<td>Haskell and Reynolds (1947)</td>
</tr>
<tr>
<td>TAE (time of breeding activity)</td>
<td>8.0</td>
<td>4.0</td>
<td>Haug (1969)</td>
</tr>
<tr>
<td>TLDEL (time of litter growth effects)</td>
<td>35.0</td>
<td>3.0</td>
<td>Hammond (1965)</td>
</tr>
<tr>
<td>TWN1 (beginning of weaning period)</td>
<td>7.0</td>
<td>2.0</td>
<td>Haskell and Reynolds (1947)</td>
</tr>
<tr>
<td>TWN2 (end of weaning period)</td>
<td>20.0</td>
<td>4.0</td>
<td>Haskell and Reynolds (1947)</td>
</tr>
<tr>
<td>UE (metabolizable energy efficiency)</td>
<td>0.928</td>
<td>0.009</td>
<td>Shoemaker et al. (1976)</td>
</tr>
<tr>
<td>WK (mature body weight of juveniles)</td>
<td>2.10</td>
<td>0.15</td>
<td>Haskell and Reynolds (1947)</td>
</tr>
<tr>
<td>WPAR (parturition weight of young)</td>
<td>0.11</td>
<td>0.01</td>
<td>Haskell and Reynolds (1947)</td>
</tr>
</tbody>
</table>

a SD = range divided by 4.

b CV of 10 percent.
Appendix B

Jackrabbit Experimental Model Listing
CALL GUTS

THIS IS A DUMMY CALLING PROGRAM.
STOP
END

SUBROUTINE GUTS

THIS SUBROUTINE IS THE GUTS OF THE EXPERIMENTAL MODEL AND INCLUDES

CONTROLS PROGRAM FLOW AND TIMING OF EVENTS AS WELL AS UPDATING

NUTRITIONAL VARIABLES.

INTEGER T, DT, TCON, TPART, GEST, TEND, TSTART, TDEDEL, TA1, TA2, TNN1, TNN2,

* ALITS

REAL ME, EMEDIE, LACRFD, LJRATE, NFMLK, LINC

DIMENSION XP(52), YP(10, 52), X(8, 400), PH(8, 400), CAH(52), CADF(52),

YM(2, 52), YS(2, 52), YS(2, 52),

DIMENSION TGER(400), KT(8), DP(15), CDP(15), DP(15), DCPD(15),

IP(16), RPI(16), DDF(16), WP(71), WPD(71), WP(71), WPD(71), DLITS(8), DLITS(8),

UPE(15, 10), DCP(15, 10),

COMMON/ BFET(8, 400), PWXFT(8, 400), WYNQ(8, 400), PWWQ(8, 400),

UV(8, 400), PWUV(8, 400), LITS(8), HADML(400), MADF(400), PWW(8),

PHIU(8), G(15, 10), CXP(15, 10), DIT(15, 10), CDPD(15),

COMMON/T, DFP, RDP, RDP(15), CP(15, 10), CDPD(15),

COMMON/ RFDH(8), TDFD(8), FNSY(8), ESY(8), DCPY(8), PBH(8), RFQJ(8), TQD(8),

FQDJ(8), EBDJ(8), DCPY(8), DPHJ(8), PH(8), EMB(8), EMB(8), PHB, TNNR, TNNR,

COMMON/ TOP, TTPR, TDEDEL, TSTR, LAG, Gest, TA1, TA2, TNN1, TNN2, TCR, ITD, IT5,

* IFT, IFSIT, TCON, LITMAX

EQUIVALENCE (TOP, IP(1))

COMMON/C/ C, C/N, RPN, FPN, HATPN, HP2, GEMLK, CMFN, CNg, PP1, PP2, LINC, LINC,
C.*ALL INPUT VARIABLES, INITIAL CONDITIONS AND FINAL PARAMETER VALUES

C.*ARE ECHO PRINTED TO CHECK THE CONDITIONS FOR A RUN.

WRITE(b,10002)
10002 FORMAT('DO 150 I=1,16
DO 150 I=1,16
150 IP(I)=RT(RIP(I),DIP(I),IR)
DO 150 I=1,17
151 RP(I)=RR(RWP(I),DHP(I),IR)
DO 150 I=1,LITMAX
152 LITS(I)=RI(RLITS(I),DLITS(I),IR)
IF(LITS(I),LT,1) LITS(I)=1
CON(I)=CON1
DO 6 L=2,LITMAX
6 CON(L)=CON(L-1)+GEST+IUP
READ(1,2020)AV
DO 154 I=1,365
DO 150 K=1,9
154 V(I)=V(I-1)+AV(I,K)
C.*ALL INPUT VARIABLES, INITIAL CONDITIONS AND FINAL PARAMETER VALUES

C.*ARE ECHO PRINTED TO CHECK THE CONDITIONS FOR A RUN.

WRITE(b,10002)
10002 FORMAT('DO 150 I=1,16
DO 150 I=1,16
150 IP(I)=RT(RIP(I),DIP(I),IR)
DO 150 I=1,17
151 RP(I)=RR(RWP(I),DHP(I),IR)
DO 150 I=1,LITMAX
152 LITS(I)=RI(RLITS(I),DLITS(I),IR)
IF(LITS(I),LT,1) LITS(I)=1
CON(I)=CON1
DO 6 L=2,LITMAX
6 CON(L)=CON(L-1)+GEST+IUP
READ(1,2020)AV
DO 154 I=1,365
DO 150 K=1,9
154 V(I)=V(I-1)+AV(I,K)
CONTINUE
DO 40 K=1,NNL
KT(K)=KT(K)+1
IF(K(K),GE,TPART(LITMA)+1,TPR)GO TO 40
C...DETERMINE THERMOREGULATION OF YOUNG.
CALL HEAT(PYNG(K,T),TEMP,BHP,THP)
C...DETERMINE ACTIVITY OF YOUNG.
IF(T,LT,TPART(K)+TAT)AFY=AYA
IF(TPART(K),TA,LE,T,AND,T,LE,TPART(K)+GEST)AFY=AYAH+AYC*(T-TPART(K))
C...DETERMINE POTENTIAL TISSUE GROWTH OF LITTERS.
TISERY=PHYT(K)*GREA*DPY
IF(DFUG,EG,2)=RTC(0,T),T,THP,DERY,TISERY
C...TOTAL DAILY ENERGY REQUIREMENTS OF YOUNG
DERY(K)=DERY*TISERY
C...SIMULATE WEANING.
IF(T,LT,TPART(K)+THN1)RD(K)*RDA
IF(TPART(K)+THN1,LE,T,AND,T,LT,TPART(K)+THN2)RD(K)=RUR-RDC*(T-TPAR(K))
C...PRODUCTION ENERGY REQUIREMENTS FOR ADULT FEMALES
C FOR GESTATION, ADULT FEMALES ONLY
TGR=GP1*PAR+GP2
FA=PFET(NLIT,T)/HAP
IF(FHA,GT,1)FHA=1
FTGK(T)=FHA*FTGKLAITS(NLIT)
IF(T,EG,TSTART)GO TO 35
GER=GER(T)=FTGFP(T-0T)
GER=GER(T)=GER+0.0
IF(DFUG,EG,2)WHITE(0,T),FTGER(T),FTGER(T-DT),GER,F=A
C FOR LACTATION, BASED ON NEEDS OF OFFSPRING, FOR ADULT FEMALES ONLY
35 IF(T,LT,TPART(K)+11)GO TO 40
DEH=(TOFHY(NNL))*RD(NNL)/NMLX*LITSNL
IF(DFUG,EG,2)WHITE(0,T),RD(NNL),DERL
POMP(T)=DERL/GFMLK
DMP(T)=DMP(T)
C...Milk Nitrogen Content SFT.
RM=N+MN
C...TOTAL DAILY ENERGY REQUIREMENT, BOTH SEXES
C...Determine where intake requirements are determined, based on energy require-
IF(T,GF,TCON(1),AND,T.LE.TPART(LITMAX))GO TO 51
GO TO 52
C*.FORAGE INTAKE MODIFIED BY INTAKE INCREASES, BASED ON SEASON.
51 FDINM=RFDM*RFDF*FDIM
52 IF(T,GT,TPART(LITMAX-2))FDINM=RFDM*(1.+FDIM)
53 FDINM=RFDF*RFDF*FDIM
54 CONTINUE
55 IF(T,GT,TPART(LITMAX-2),AND,MON,LT,9)FDINM=RFDF*RFDF*FDIM
56 IF(MON,GT,9)FDINM=RFDF*RFDF*FDIM
57 IF(TCON(LITMAX)+180,LT,9,AND,T,LT,TCON(LITMAX)+180)GO TO 53
58 GO TO 54
59 FDINM=RFDM*(1.+FDIM)
60 FDINM=RFDF*(1.+FDIM)
61 FDINM=RFDM*RFDF*FDIM
62 CONTINUE
C*.FORAGE INTAKE MODIFIED BY RELATIVE AVAILABILITY OF HERBAGE AND
C*.POPULATION DENSITY.
63 RAV=V(T)
64 IF(I,RAV,FQ,.1)GO TO 255
65 IF(I,RAV,FQ,.2)GO TO 255
66 GO TO 256
67 IF(T,GT,TPOP)RAV=V(T)/TPOP
68 GO TO 256
69 IF(T,GT,TPOP)RAV=V(T)/TPOP
70 CONTINUE
71 IF(IF,RAV,FQ,.1)CONSUM=CMax
72 IF(IF,RAV,FQ,.2)CONSUM=CMax*(RAV/(RAV+CONA))
73 IF(IF,RAV,FQ,.3)CONSUM=CMax*(1.-EXP(-CONB*RAV))
74 IF(IF,RAV,FQ,.4)CONSUM=CMax/(1.+CONC*EXP(-COND*RAV))
75 IF(IF,RAV,LT,T5)GO TO 55
76 IF(RAV,LE,CONNM)CONSUM=CONS*RAV
77 IF(RAV,GT,CONNM)CONSUM=CMax
78 55 CONTINUE
79 IF(IF,RAV,FQ,.1)FDINM=CONSUM*FDINM
80 IF(IF,RAV,FQ,.2)FDINM=CONSUM*FDINM
81 IF(IF,RAV,FQ,.3)FDINM=CONSUM*FDINM
82 IF(IF,RAV,FQ,.4)FDINM=CONSUM*FDINM
83 C*.GROSS ENERGY INTAKE
84 C*.ENERGY CONTENT OF INTAKE DETERMINED.
85 GEIN=FDINM*GEDIET(MON)
86 GEIN=DIG*UF
87 C*.INITIAL ENERGY BALANCE OF MALES DETERMINED.
88 EBM=EMF*DERM
89 EDUH=EFB*TDERM/DERM
90 EDUH=FDINM*GEDIET(MON)
91 GEIN=DIG*UF
92 C*.INITIAL ENERGY BALANCE OF FEMALES DETERMINED.
93 EBF=EMF*DERF
94 EDUH=EFB*TDERF/DERF
95 IF(IFDEBUG,FQ,.3)WRITE(b//)T,FDINM,FDINM,EBM,EBF
96 TFDFINM=FDINM*FDINM
97 TFDFDFINM=FDINM
98 IF(T,GT,TEND-1)GO TO 5075
99 GO TO 5076
5075 AFDFINM=TFDFINM/FLOAT(TEND)
5076 AFDFINM=TFDFINM/FLOAT(TEND)
5077 FORMAT(1'0',1'T',13,'2',"A'FDINM",13,'2',"AFDFINM",13,'2',"AFDFINM",13,'2',"AFDFINM",13,'2',"AFDFINM")
5078 CONTINUE
C*.PROTEIN REQUIREMENTS, BASED ON FOOD INTAKE REQUIRED FOR ENERGY BALAN-
C....ADULT MALES
CPD pig*CPD M)==0
C..CRUDE PROTEIN INTAKE DETERMINED,
CPD * 1PD/CPD: M)/(100,)*CPDIG
C..NITROGEN BALANCE SUBROUTINE CALLED TO DETERMINE DAILY PROTEIN
CALL NALC(MAD(T),RFOM,LL)
DCPRM + TONHF+RATPN
C..PROTEIN BALANCE DETERMINED FOR MALES.
PB=CPIN=DCPRM
PDUM=CPIN/DCPRM
C..PROTEIN LIMITATIONS CALCULATED AS A FRACTION OF REQUIRED PROTEIN
PRF=PRF/DCPRM
C..FINAL RATE VALUES FOR CHANGES IN ADULT MALE
C..BODY WEIGHTS AND UPDATES WADM LEVEL.
C..CRUDE PROTEIN INTAKE DETERMINED,
CPD * 1PD/CPD: M)/(100,)*CPDIG
C..NITROGEN BALANCE SUBROUTINE CALLED TO DETERMINE DAILY PROTEIN
CALL NALC(MAD(T),RFOM,LL)
DCPRM + TONHF+RATPN
C..PROTEIN BALANCE DETERMINED FOR FEMALES.
PB=CPIN=DCPRM
PDUM=CPIN/DCPRM
PLIM I=(PB/DCPRM)
IF(PBF,GE,0,)=1PLIM I=1
FETRFD=1.0
IF(DFUG,EG,8,)=WRITE(6,/) T,CPIN,DCPRM,PRF,PLIM
C..ONLY IF FEMALES ARE PREGNANT OR LACTATING ARE THESE OPTIONS EXCLUDED
IF(GET,LF,0,AND,DFRL,LL,0,)=GO TO 70
IF(PRIG,GE,0,AND,EHF,GE,=,HAL)=GO TO 71
GO TO 72
C..EXCESS PROTEIN IS CATABOLIZED FOR ENERGY.
PB*PB/1000,=FPRO)
C..PROTEIN
72 IF(PB,GE,0,AND,EHF,GE,=,HAL)=GO TO 71
GO TO 72
C..LACTAL REPRODUCTIVE ENERGY IS CALIBRATED AND THE TOTAL REDUCTION IN
C..REPRODUCTIVE OUTPUT IS DETERMINED.
75 ELAR=GEN+DFRL
IF(ELAR,GE,0,)=GO TO 77
IF (ELAB, LT, FBSPF) GO TO 69
E1*GER/ELAB
F2*DEPL/FLAB
TOTRED=EBF-(ERF*STOR)
C.**GESTATION ENERGY REDUCTION IS CALCULATED.
GESRED=TOTRED+F1
C.**LACTATION ENERGY REDUCTION IS CALCULATED.
LACRED=TOTRED+F2
IF (LACRED, GT, DEPL) LACRED=DEPL
IF (DEPL, LE, 0.) GO TO 76
C.**LACTATION IS REDUCED BY THE FRACTION OF THE SHORTAGE.
ERFLAC*(DEPL-LACRED)/DEPL
DMP(T)*POMP(T)*ERFLAC
76 IF (GER, LE, 0.) GO TO 79
C.**GESTATION IS REDUCED BY THE FRACTION OF THE SHORTAGE.
GESRED*(GER-GESRED)/GER
C.**FETAL GROWTH REDUCTION IS THE MINIMUM OF PROTEIN AND ENERGY
C.**RESTRICTIONS.
FETRED=MIN1(GESRED, PLIM)
GO TO 79
C.**MILK COMPOSITION IS CHANGED IF PROTEIN IS LIMITING.
75 RMN#RR#RRMN
FETRED=PLIM
C.**MADE.
448 EBF=EBF*TOTRED
449 GO TO 70
450 69 ERFLAC=1,0
451 GESRED=1,0
452 FETRED=1,0
453 PLIM=1,0
454 C.**THIS SECTION DETERMINES FINAL RATE VALUES FOR BODY WEIGHT CHANGES OF C.**FEMALES AND UPDATES MADE LEVEL.
70 IF (ELAB, LE, EBF, AND, EAF, LE, ELAB) RATE=0.
IF (EBF, GT, ELAB) RATE=EBF/(GERS/GERS)
77 IF (EBF, LT, ELAB) RATE=EBF*(EBF*CAT)/(EFAT*DRY)
459 IF (DEBUG, EQ, 9.9) WRITE (9,/) , ELAB, E1, E2, GESRED, LACRED, TOTRED, EBF
460 MADF (T+DT) = MADF (T) * DT/RATE
461 IF (MADF, LE, 0.) GO TO 102
462 IF (DEBUG, EQ, 0.9) WRITE (9,/) , TNIT, TNL
463 IF (T, LT, TCON(NLTL) OR, T, GF, TPART(NLTL)+T) GO TO 102
464 IF (DEBUG, EQ, 10.9) WRITE (9,/) , T, AFET, TNL, TFRATE, TFRAT, TFRAT
465 *FET(NLTL, T+DT) = FET(NLTL, T) * DT/RATE
466 102 CONTINUE
467 IF (DEBUG, EQ, 10.9) WRITE (9,/) , T, YNG(NLTL, T), WJUV(NLTL, T)
468 EMLKCN=0,0
469 PLMLKCN=0,0
470 C.**THIS SECTION DETERMINES THE GROWTH PATTERNS OF SUBADULTS, RASFD ON C.**POSSIBLE GROWTH AND WHATEVER NUTRITIONAL RESTRICTIONS APPLY.
471 DO 101 KK=1,NNL
473 IF (T, LT, TPART(1)) GO TO 101
474 IF (T, GT, TPART(LTMAX)+1) OR (K) GO TO 108
475 C.**..........YOUNG
476 IF (KK, EQ, NN1) GO TO 103
477 GO TO 104
478 C.**ENRGY AND PROTEIN CONTENT OF THE MILK CONSUMED IS CALCULATED.
479 103 EMLKCN=(DMP(T)/LIT (NNL)) * GEML*K*EMLK
CALL NRAL(PPJUV(KK),T),RF,KK)
OCPRJ(KK) = TDRNJ(KK) + PATPN
C..Protein Balance of Juveniles Determined.
PBJ(KK) = (CPIN - OPCPRJ(KK))
FDUJ(KK) = (CPIN - OPCPRJ(KK))
IF DEBUG, EQ, 6, 8 WRITE (b, 7) T, KK, OPCPRJ(KK), PBJ(KK)
IF (T, LT, TPART(KK) + IBPK) GO TO 117
IF (DEBUG, EQ, 6, 8) WRITE (b, 7) T, KK, OPCPRJ(KK), PBJ(KK)
IF (T, LT, TPART(KK) + IBPK) GO TO 117
C..Protein energy reduction factors of young determined.
PBJF = (1.0 * PBJ(JK) / OPCPRJ(KK))
ERJF = (1.0 * EBJ(KK) / TDRERJ(KK))
IF DEBUG, EQ, 6, 8 WRITE (b, 7) T, KK, PRJF, ERJF, JSRAT(KK)
C..final rate values determined for juveniles as a function of potential
C..rates, and reduction factors.
IF (PBJ(KK), GE, 0.0) GO TO 116
IF (ERJF(KK), GF, 0.0) JSRAT(KK) = PRJF
IF (ERJF(KK), LT, 0.0) JSRAT(KK) = PRJF * ERJF
IF (DEBUG, EQ, 6, 8) WRITE (b, 7) T, KK, JSRAT(KK), EBJ(KK)
GO TO 117
116 IF (PBJ(KK), GE, 0.0) JSRAT(KK) = PBJ(KK) / 1000.0 * EPRO
IF (PBJ(KK), GF, 0.0) JSRAT(KK) = PBJ(KK)
IF (PBJ(KK), LT, 0.0) JSRAT(KK) = 1.0
IF (EBJ(JK), GF, 0.0) JSRAT(KK) = EBJ(JK) * JSRAT(KK)
IF (DEBUG, EQ, 6, 8) WRITE (b, 7) T, KK, JSRAT(KK), EBJ(KK)
117 CONTINUE
C..This section updates level values of wyng and wjuv based on the above
C..determined rates.
IF (T, EQ, TPART(KK)) GO TO 110
IF (T, GE, TPART(KK) + IBPK) GO TO 111
WYNG(KK, T = DT) = WYNG(KK, T) + DT * JSRAT(KK)
GO TO 111
110 WYNG(KK, T = DT) = WYNG(KK, T) + DT * JSRAT(KK)
GO TO 110
112 WYNG(KK, T = DT) = WYNG(KK, T) + DT * JSRAT(KK)
101 CONTINUE
IF (DEBUG, EQ, 6, 8) GO TO 130
GO TO 131
130 IF (MON = 30, EQ, 12) WRITE (b, 7) T, EBF, PBH
IF (T, MON = 30, EQ, 12) WRITE (b, 7) T, EBF, PBH
IF (PBPM(T), GE, 0.0) WRITE (b, 7) T, EBF, PBH
131 CONTINUE
C..population submodel is called here to calculate population response.
C..call popxx(dug)
C..this section calculates the total forage consumption of the population
C..and the fraction that this consumption comprises of available forage
C..forage.
QUAN = 0.0
QSUB = 0.0
GO 500 J = 1, LIMIT
Q = DYNG(J, T) * FDNJ(J) / 1000.
Q = QDNUV(J, T) * FDNJ(J) / 1000.
Q = QSUB(J) + QU + QY
Q = QDADM(T) * FDNM / 1000.
Q = QDADF(T) * FRFD / 1000.
QUAN = QM + GF + QSUB
DEP = (QUAN / V)(T)
DEP2=QUAN/RAV
IF(DEBUG.EQ.1.)WRITE(b/1,T,QM,GF,GSUR,QUAN,DEP1,DEP2)
C........INCREASE TIME
3 T=T+DT
C........ARE LOOPS FINISHED?
IF(I.GT.FEND)GO TO 20
GO TO 2
20 CONTINUE
C........WRITE RESULTS AND STORE FOR PLOTTING
IF(DEBUG.GT.0.)GO TO 37
DO 26 JW=1,LITMAX
DO 26 J=1,TEND
IF(PWJUV(J,J),NE,0.)PW(J,J)=PWJUV(J,J)
IF(PWYNG(J,J),NE,0.)PW(J,J)=PWYNG(J,J)
IF(PMUV(J,J),NE,0.)PM(J,J)=PMUV(J,J)
IF(PMUV(J,J),NE,0.)PM(J,J)=PMUV(J,J)
IF(WFET(J,J),NE,0.)WF(J,J)=WFET(J,J)
IF(WFET(J,J),NE,0.)WF(J,J)=WFET(J,J)
CONTINUE
IF(BUG.EQ.1.)GO TO 132
GO TO 133
C........WRITE WEIGHTS OF YOUNG AND JUVENILES.
132 WRITE(b,1024)
1024 FORMAT('IN','$WYNG(K,T)\$')
DO 134 J=1,TEND
WRITE(b,1005),WYNG(J,J),J=1,LITMAX
WRITE(b,1025)
1025 FORMAT('IN','$WJUV(K,T)\$')
DO 134 J=1,TEND
WRITE(b,1005),WJUV(J,J),J=1,LITMAX
C........WRITE WEIGHTS OF ADULT MALES AND FEMALES.
WRITE(b,1011)
DO 135 J=1,TEND
WRITE(b,1008),WADM(J),J=1,ADF
135 CONTINUE
IF(BUG.EQ.2.)GO TO 24
GO TO 37
24 WRITE(b,1017)
IS=PART(J,T)+1
IX=PART(J,LITMAX)+35
DO 44 J=1,33 IT=S,J+DT
44 CONTINUE
C........WRITE POTENTIAL AND REALIZED MILK PRODUCTION.
33 WRITE(b,1008),POMP(J)
WRITE(b,1010)
DO 44 J=1,33 IT=S,J+DT
31 WRITE(b,1008),DMP(J)
1K=TEND/INT
C........PLOT POTENTIAL AND REALIZED MILK PRODUCTION.
DO 122 J=1,INT
2 TM=INT
XP(J)=T
YM(J)=POMP(J)
122 YM(J)=DMP(J)
C........CALL PLOTS
IF(GRAPH.EQ.1.)CALL PLOTS(2,INK,XP,YM,P)
DO 137 J=1,2N+2,DT
IS=PART(J,LITMAX)+1+1
XP(J)=T
YM(J)=POMP(J)
CALL PLOTS(2, INK, XP, YM, 2)

C.. END OF.FALSEimonials

RETURN
SUBROUTINE POPIN (UG, TSTART, TEND, LITMAX, IR)

INTEGER T, DT, TCON, TPAR, GFST, TEND, TSTART, Tdel, TAI, TAP, TWN1, TWN2,

*ALITS

DIMENSION DPREG(A), COMMON/POP/DFE(T,8,400), PREG(8), ALIT(S,8,400), TSNR(8,400), DSUR(8,400),

*SPOR, FPOP, AGE, TAD(400), PREMOR, CJM, CHM, CASN, DAM(400), DADF(400),

*DYNG(8,400), DJUV(8,400), IRR, SEXR, TOP, CDEN, EDUF, PDUF, EDUM, PDUM,

*EDU(8), PDU(A), EDU(A), PDU(A), SF1, SF2, SF3, CHMNAT, CHMPRO, CMFPRD,

*CWMN, CASMT, CASHD, CASMN, CJMPR, CJM

PARAMETER MEAN AND STANDARD DEVIATIONS INPUT,

READ(7,2011) PPREMOR, DPREMO
READ(7,2011) CWMNAT, DCWMNA, CWMPRD, CMFPRD, CMFPRH
READ(7,2011) CASMT, DCASMT, CASHMD, DCASMP
READ(7,2011) CWMNAT, DCWMNA, CJMPR, DCJMPR
READ(7,2012) CWMN, CASM, CJMN
READ(7,2011) SEXR, DSEXR
READ(7,2013) IRRKII, DIRRKII
READ(7,2013) (PREG(I), I=1, LITMAX)
READ(7,2013) (DPREG(I), I=1, LITMAX)
READ(7,2013) DAM(TSTART), DADF(TSTART)
READ(7,2013) CDEN, DCDEN
READ(7,2013) SF1, SF2, SF3

STOCHASTIC PARAMETER GENERATOR CALLED TO DETERMINE FINAL PARAMETER

VALUES BASED ON MEAN AND STANDARD DEVIATIONS,

PPREMORRR(PREMOR, DPREMO), IR)
CWMNATRR(CWMNAT, DCWMNA, IR)
CMFPRDRR(CMFPRD, CMFPRH, IR)
CASMTRR(CASMT, DCASMT, IR)
CASMPDRR(CASMPD, DCASMP, IR)
CJMPRRR(CJMPR, DCJMPR, IR)
SEXRRR(SEXR, DSEXR, IR)
CDENRRR(CDEN, DCDEN, IR)
IRRKIIIRR(IRRKII, DIRRKII, IR)
DO 250 I=1, LITMAX
PREG(I)RRR(PREG(I), DPREG(I), IR)

ECO PRINT FINAL POPULATION PARAMETERS FOR THE RUN,

WRITE(6,2003)
WRITE(6,2002)
WRITE(6,2003)
WRITE(6,2002)
WRITE(6,2003)
WRITE(6,2002)
WRITE(6,2003)
WRITE(6,2002)
WRITE(6,2003)
WRITE(6,2002)
WRITE(6,2003)
WRITE(6,2002)
WRITE(6,2003)
C. SET POPULATION VARIABLE INITIAL CONDITIONS.

200 DO 301 I=1,LITMAX
201 DO 302 J=1,TEND
202 ALITS(I,J)=0
203 DFT(I,J)=0.
204 DYNG(I,J)=0.
205 907 TSSUB(J)=0.
206 TAD(J)=0.
207 302 DJUV(T,J)=0.
208 301 CONTINUE
209 TAD(TSTART)=DADM(TSTART)+DAF(TSTART)
210 TPOP=TAD(TSTART)
211 WRITE(b,2014)
212 2014 FORMAT(10,1,JAN 1 DENSITY PER KM^2 OF ADULT MALES AND FEMALES!)
213 202 FORMATO(1,1,MORTALITY RESPECTIVELY, BY YEAR!)
214 203 FORMATO(10,1,PREGNATAL,IR--=OCT JUV, WINTER ADULT AND SUMMER ADULT!)
215 204 FORMAT(10,1,6)
216 205 FORMAT(10,1,3)
217 206 FORMAT(10,1,3)
218 207 FORMATO(1,1,RESULTS OF THE SIMULATION-- NUTRITION!)
219 208 IF(DUG.EQ.23.)WRITE(b,/)PRENATAL, PREG, TAD, TPOP
220 209 RETURN
221 210 END

C. SUBROUTINE POPEX(DUG)

C. THIS SUBROUTINE EXECUTES THE CHANGES IN POPULATION DENSITY OF LIFE

C. HISTORY STAGES AS A FUNCTION OF NUTRITIONAL DYNAMICS AND PREDATION,

C. INTEGER T, DT, TCP, TDY, TEND, TSTART, TDEL, TAA, TAD2, TNN, TNN2, TNN3

C. ALITS

C. COMMON/POP/DTET(R,400), PREG(A), ALITS(B,400), TSSUB(400), DSUB(R,400),

C. SPOT, POP, AGF, TAD(400), PHEMON, CJMN, CMNN, CASHM, DADM(400), DAF(400),

C. DYNG(A,400), DJUV(A,400), ITDKIT, SEXR, TPOP, CMEN, EDUF, PDUF, EDOM, PDUM,

C. EDUV(A), PDUV(A), FDUJ(A), PDUJ(R), SF1, SF2, SF3, CMNNAT, CMNPRD, CFMND

C. CMNN, CASHMN, CASHMP, CSMN, CJMPRD, CSMN2, CJMN

C. COMMON/FEET(R,400), PFEET(A,400), PYNG(A,400), PXYNG(R,400),

C. JUV(R,400), PÅJUV(A,400), LITS(R), HADM(400), AHDF(400), PWMY(A),

C. PWMY(A), CE(1,10), CP(1,10), DTET(15,10), GEDSET(15,10), CPDSET(15),

C. UNP(400), VPN(400), RD(8), FRATE, BRATE, DRATE, YRATE (R),

C. KFNY(A), TEDY(R), FDNY(N), EHY(H), ECRNY, DCFNY(1,10), PHY(B), RFDJ(A),

C. DFKJ(B), EBH(A), DFKJ(R), PBH(B), EBH, ERP, EBF, EBF, TDKR, TDNR,

C. TDNYK(A), TDNYK(R), AV(365,3), V(365)

C. COMMON/1,T, TSTART, TEND, TDEL, TAA, T2, TNN, TNN2, TNN3, ICR, IT4, IT5,

C. TT, IATT, TCP, TDY, TMAX

C. IF(DUG.EQ.23.,AND,1,TT,TSTART)WRITE(b,/)PRENATAL,TAD, TPOP

C. IF(T,LT,TCON(1))GO TO 320

C. IF(T,GT,TCON(NLIT))GO TO 396

C. GO TO 386

C. DESCRIPTION OF FUTURES IS DETERMINED.

C. 306 HCFTDADOS(T),PREG(NLIT),LITS(NLIT)

C. IF(DUG.EQ.20,)WRITE(b,/)TDAFT(T),PREG(NLIT),LITS(NLIT)

C. DFTDHCFTDUT

C. GO TO 310

C. IF(AILTS(NLIT,T),FD,0)ALITS(NLIT,T),LITS(NLIT)

C. IF(DUG.EQ.20.,WRITE(b,/)T,NLIT,LITS(NLIT),ALITS(NLIT)

C. NUTRITIONAL DEFICIENCY UNITS APPLIED TO PRENATAL MORTALITY ARE THE

C. MINIMUM OF ADULT FEMALE ENERGY AND PROTEIN DEFICIENCY UNITS.
**Generic Programming Code Snippet**

```plaintext
DBM*NINI(EDUF, PNUF)
SP*(1., PREMOR) - SFRAC(DU, SF1, SF2, SF3)
PREMOR*1. - SP
C*, FLOW RATE OF FETUSES DETERMINED AND DFET LEVEL UPDATED.
DFET = PREMOR * DT * DFET(NLIT, T) + DFLO * PREG(NLIT) * ALTS(NLIT, T)
IF (DUG.EQ.20.) WRITE(b2, I)
305 DFET(NLIT, T + DT) = DFET(NLIT, T) + DT * DFLO
ALTS(NLIT, T + DT) = DFET(NLIT, T) / (DAFT(T) * PREG(NLIT))
IF (T, LT, TPART(1)) GO TO 320
C*, THIS SECTION DETERMINES THE DENSITY CHANGES OF EACH COHORT OF
C*, SUBADULTS HORN. INDIVIDUALS ARE CLASSIFIED AS YOUNG UNTIL IRKT,.
C*, THEN AS JUVENILES.
GO TO 320, KK = 1, ANL
IF (T, LT, TPART(1), OR, T, GT, TPART(LTMAX) + IBKII) GO TO 330
IF (T, GE, TPART(KK) + IBKII) GO TO 330
IF (T, EQ, TPART(KK)) GO TO 307
GO TO 308
C*, RECRUITMENT OF YOUNG DETERMINED.
RCYNG = DFET(KK, T)
IF (DUG, EQ, 21, ) WRITE(a, /), T, KK, DFET(KK, T)
DFLO = RCYNG / DT
GO TO 309
C*, THE RELATIVE FLOW RATE OF YOUNG DENSITY IS DETERMINED BY YMORT.
308 DYFLO = YMORT(KK) * DYNG(KK, T)
IF (DUG, EQ, 21, ) WRITE(b, /), T, KK, DFLO, DYNG(KK, T)
C*, DYNG LEVEL IS UPDATED.
309 DYNG(KK, T + DT) = DYNG(KK, T) + DT * DFLO
GO TO 320
C*, RECRUITMENT OF JUVENILES IS DETERMINED.
330 RCJUV = DFET(KK, T)
GO TO 333
332 RCJUV = DYNG(KK, T)
IF (DUG, EQ, 22, ) WRITE(a, /), T, KK, DFLO, DYNG(KK, T)
GO TO 334
C*, THE RELATIVE FLOW RATE OF JUVENILE DENSITY IS DETERMINED BY YMORT.
333 DFJLO = YMORT(KK) * DJUV(KK, T)
IF (DUG, EQ, 22, ) WRITE(b, /), T, KK, DFLO, DJUV(KK, T)
GO TO 336
C*, DJUV LEVEL IS UPDATED.
334 DJUV(KK, T + DT) = DJUV(KK, T) + DT * DFJLO
GO TO 320
C*, THE RELATIVE FLOW RATE OF HALF DENSITY IS DETERMINED BY AMMORT.
336 DADF = AMMORT(IJK) * DADM(T)
IF (DUG, EQ, 23, ) WRITE(a, /), T, DFJLO, DADM(T)
C*, DADM LEVEL IS UPDATED.
338 DADM(T + DT) = DADM(T) + DT * DADF
C*, THE RELATIVE FLOW RATE OF FEMALE DENSITY IS DETERMINED BY ASMRT.
339 DADF = ASMRT(IJK) * DADF(T)
IF (DUG, EQ, 23, ) WRITE(b, /), T, DFJLO, DADF(T)
C*, DADF LEVEL IS UPDATED.
341 DADF(T + DT) = DADF(T) + DT * DADF
C*, THIS SECTION CALCULATES THE SUBADULT, ADULT AND TOTAL POPULATION
C*, DENSITY.
GO TO 340, IE = LTMAX
GO TO 341
IF (DYNG(I, T + DT), NE, 0) TSUR(I, T + DT) = DYNG(I, T + DT)
IF (DJUV(I, T + DT), NF, 0) TSUR(I, T + DT) = DJUV(I, T + DT)
TSUR(T, T + DT) = TSUR(T + DT) + TSUR(T, T + DT)
GO TO 343
TSUR(T + DT) = DADM(T + DT) + DADF(T + DT)
GO TO 343
GO TO 340, IE = LTMAX
```

---

**Notes:**
- The code snippet appears to be a program for simulating population dynamics, specifically focusing on the flow rates and levels of various cohorts (fetuses, young, etc.) within a population model.
- The code includes decision-making processes based on various conditions, such as density calculations and cohort transitions.
- It uses logical operators (IF, WRITE) and arithmetic operations (WRITE, GO TO) to update variables and control flow within the simulation logic.
C..THE FOLLOWING FOUR FUNCTIONS WERE SET UP TO CALCULATE MORTALITY RATES
C..AS A FUNCTION OF NUTRITIONAL DEFICIENCIES AND PREDATION, AS THEY
C..EXIST PRESENTLY THE FUNCTIONS FOR YOUNG AND JUVENILES AND FOR MALES
C..AND FEMALES ARE IDENTICAL. AS MORE DATA IS ACCUMULATED THESE
C..FUNCTIONS CAN BE DIFFERENTIATED.

C..FUNCTION VMORT(KK)

C..THIS FUNCTION DETERMINES MORTALITY RATE OF YOUNG.
INTEGER T,DT,TCON,TPART,GEST,TEND,TSTART,TDEL,T1,T2,TOWN1,TOWN2,
*ALITS
COMMON/POP/DFET(8,400),PERSON(8),ALITS(8,400),TSUR(400),DSUR(4,400),
*DROP,POP,AGE,TAD(400),PREMOR,CM,CMH,CASHM,DADF(400),DADF(400),
*DYNG(8,400),DUJV(A,400),I8KTI,SEXH,TPDP,CDEN,EDUF,POUF,EDUM,
*EDU(8),PDU(8),PDUJ(8),PDUJ(8),SF1,SLF2,SLF3,CMHNT,CMHDP,CMHPO,CMHDP,
*CMHN,CMASNT,CMASPI,CMSN,CMJNT,CMJPPO,CMJJPPO,CMJNPPO,CMJNPPO,
*COMMON/AMB/AMTET(8,400),PMEFET(A,400),PMHTG(8,400),
*HJUV(8,400),HJUJ(8,400),LITS(8),HADM(400),HADF(400),PHJY(4),
*PHIJ(8),GE(15,10),CP(15,10),UJET(15,10),GDDET(15),CPDET(15),
*DNPH(400),PDNPH(400),RD(8),RATE,RALET,DRATE,RAV(4),RATE(8),
*RFDY(8),TDENS(8),FDYN(8),EBY(8),DFPRY(8),DFPRY(8),FDJ(8),TDJ(8),
*FCJNJ(8),EJN(8),DFPRY(8),DFPRY(8),EBN,EBF,EBF,EBF,EBF,EBF,EBF,EBF,
*TDJN(8),TDJN(8),AV(365,9),V(365),
*COMMON/VE/DT,TSAT,TDAT,DTNL,DMON,TCON(8),TPART(8),
*COMMON/VE/POP,TPRO,TVDEL,LAG,GEST,T1,T2,TOWN1,TOWN2,ICR,IT4,ITS,
*ITT,TTTT,TCON1,TLMAX

C..INTERVAL FINITE SURVIVAL IS THE EXPONENTIAL OF INSTANTANEOUS
C..MORTALITY.

C..NATURAL MORTALITY.
SCJNP=EXP(-JCJHP)
C..TIME STEP FINITE SURVIVAL IS DEPENDENT UPON THE LENGTH OF THE LIFE
C..HISTORY STAGE.
SNAT=SCJNP*(1/CJHP)
C..NATURAL SURVIVAL IS MODIFIED BY ENERGY AND PROTEIN DEFICIENCY UNITS
DUWAMNI=EDY(XX),PDUY(XX)
XSJRAT=SFPTU(OU,SLF1,SLF2,SLF3)
C..MODIFIED INSTANTANEOUS MORTALITY IS THE NEGATIVE LN OF FINITE
C..SURVIVAL.
YNAT=ALOG(KK*JCJHP)
C..TOTAL FINITE MORTALITY RATE IS THE EXPONENTIAL OF THE INSTANTANEOUS
C..AND PREDATION RATES COMBINED.
STM=EXP(-YNAT*(CMJHP))
C..THE FINAL FINITE RATE IS CALCULATED FOR THE TIME STEP.
VMORT=(1.-((STM*(1/CJHP))))/DT
RETURN
END

C..FUNCTION VMORT(KK)
C..THIS FUNCTION CALCULATES MORTALITY RATES OF THE JUVENILES.
INTEGER T,DT,TCON,TPART,GEST,TEND,TSTART,TDEL,T1,T2,TOWN1,TOWN2,
*ALITS
COMMON/POP/DFET(8,400),PERSON(8),ALITS(8,400),TSUR(400),DSUR(4,400),
*DROP,POP,AGE,TAD(400),PREMOR,CM,CMH,CASHM,DADF(400),DADF(400),
*DYNG(8,400),DUJV(A,400),I8KTI,SEXH,TPDP,CDEN,EDUF,POUF,EDUM,
*EDU(8),PDU(8),PDUJ(8),PDUJ(8),SF1,SLF2,SLF3,CMHNT,CMHDP,CMHPO,CMHDP,
*CMHN,CMASNT,CMASPI,CMSN,CMJNT,CMJPPO,CMJJPPO,CMJNPPO,CMJNPPO,
*COMMON/AMB/AMTET(8,400),PMEFET(A,400),PMHTG(8,400),
*HJUV(8,400),HJUJ(8,400),LITS(8),HADM(400),HADF(400),PHJY(4),
*PHIJ(8),GE(15,10),CP(15,10),UJET(15,10),GDDET(15),CPDET(15),
*DNPH(400),PDNPH(400),RD(8),RATE,RALET,DRATE,RAV(4),RATE(8),
*RFDY(8),TDENS(8),FDYN(8),EBY(8),DFPRY(8),DFPRY(8),FDJ(8),TDJ(8),
*FCJNJ(8),EJN(8),DFPRY(8),DFPRY(8),EBN,EBF,EBF,EBF,EBF,EBF,EBF,EBF,
*TDJN(8),TDJN(8),AV(365,9),V(365),
*COMMON/VE/DT,TSAT,TDAT,DTNL,DMON,TCON(8),TPART(8),
*COMMON/VE/POP,TPRO,TVDEL,LAG,GEST,T1,T2,TOWN1,TOWN2,ICR,IT4,ITS,
*ITT,TTTT,TCON1,TLMAX

C..TIME STEP FINITE SURVIVAL IS DEPENDENT UPON THE LENGTH OF THE LIFE
COMMON/B/FFET(A,400),P/FFET(A,400),WYNB(B,400),PWYNB(0,400),

*JUV(B,400),PJUV(B,400),LITS(A),WADM(400),WADF(400),P/=IV(A),

*PWIJ(B),GE(15,10),CPI(15,10),DIET(15,10),GEDI(15),CP/DIFT(15),

*OPP(400),POHF(400),PO(8),PRATF,BRATF,DRATF,HRATF(A),JRTF(8),

*RFODY(A),TDERY(B),FINY(A),EBY(A),DCPRY(A),POBY(A),PRDJ(A),TDERJ(B),

*FDINJ(B),EBJ(A),DCPRJ(A),PWIJ(B),EBM,EBF,PBM,PBF,POBM,PDNF,

*TDRNY(A),TDRNJ(B),AV(365,0),V(365)

COMMON/D/T,T,TSTART,TEND,NLIT,NNL,MON,TCON(B),TPART(A)

COMMON/A/IOP,IBRK,TLDEL,LAG,GEST,TA1,TA2,TWI1,TW2,ICR,IT4,IT5,

*ITT,TITT,TCON1,TIITMAX

C**INTerval Finite survival is the exponential of instantaneous

C**natural mortality.

SCJN=EXP(-CJMNAT)

*TIME step finite survival is dependent upon the length of the life

*HISTORY stage.

SNAT=SCJN**(1/CJMN)

C**natural survival is modified by energy and protein deficiency units

DUMAINI(EDUJ(KK),POUJ(KK))

X=SNAT*SFRAO(8,81,82,83)

C**modified instantaneous natural mortality is the negative ln of finite

C**sufficient

YNAT=ALOG**SCJN)

C**total finite mortality rate is the exponential of the instantaneous

C**natural and predation rates combined.

STP=EXP((YNAT+CJMPRO))

C**the final finite rate is calculated for the time step.

VMRIT=1.(ST**((1/CJMN))))/DT

RETURN

END

C**

FUNCTION AMMORT(IJK)

C**this function calculates mortality rates of adult males.

INTEGER T,DT,TCON,TPART,GEST,TEND,TSTART,TLDEL,TA1,TA2,TWIN1,TWIN2,

*ALITS

COMMON/PPOP/UFET(A,400),PREG(A),ALITS(A,8,400),TSUR(400),NSUR(B,400),

*SFOP,PPOP,AGE,TA0(400),PREM9,CMJ,CMJ,CMN,CASM,DADM(400),WADF(400),

*DYNG(8,400),DUVJVB(400),J8K11,SEX,FOJ,POJ,COUE,EDUJ,POUF,EDUM,POUM,

*EDUG(A),POUG(A),EDUG(A),POUG(A),SF1,8F2,8F3,CMNAT,CJMPRO,CJMPRO,

*CMN,CASM,CMJ,CMJ,CMH,CMJ,CMJ,CMJ,CMH,CMJ,

COMMON/H/FFET(B,400),PKFET(B,400),WYNK(B,400),PWYNK(0,400),

**JUV(B,400),PJUV(B,400),LITS(B),WADM(400),WADF(400),P/=IV(A),

**PWIJ(B),GE(15,10),CPI(15,10),DIET(15,10),GEDI(15),CP/DIFT(15),

**OPP(400),POHF(400),PO(8),PRATF,BRATF,DRATF,HRATF(A),JRTF(8),

**RFODY(A),TDERY(B),FINY(A),EBY(A),DCPRY(A),POBY(A),PRDJ(A),TDERJ(B),

**FDINJ(B),EBJ(A),DCPRJ(A),PWIJ(B),EBM,EBF,PBM,PBF,POBM,PDNF,

**TDRNY(A),TDRNJ(B),AV(365,0),V(365)

COMMON/D/T,T,TSTART,TEND,NLIT,NNL,MON,TCON(A),TPART(A)

COMMON/A/IOP,IBRK,TLDEL,LAG,GEST,TA1,TA2,TWIN1,TWIN2,ICR,IT4,IT5,

*ITT,TITT,TCON1,TIITMAX

C**INTERVAL finite survival is treated separately.

IF(MON,LE,3,DR,MON,GE,11)GO TO 1

IF(MON,GT,3,AND,MON,LT,11)GO TO 2

1 PRO=CJMPRO

2 PRO=CJMPRO

C**INTERVAL finite survival is the exponential of instantaneous

C**natural mortality.

SCJN=EXP(-CJNMAT)

C**TIME step finite survival is dependent upon the length of the life

C**HISTORY stage.

SNAT=SCJN**(1/CJMN)
C.. NATURAL SURVIVAL IS MODIFIED BY ENERGY AND PROTEIN DEFICIENCY UNITS
1030. DUMAM1I(EDUM,PDUM),
1031. xENNAT=SFRAc(OU, SF1, SF2, SF3)
1032. C.. MODIFIED INSTANTANEOUS NATURAL MORTALITY IS THE NEGATIVE LN OF FINITE
1033. C.. SURVIVAL
1034. AMNAT=ALOG(X**CWMN)
1035. C.. TOTAL FINE MORTALITY RATE IS THE EXPONENTIAL OF THE INSTANTANEOUS
1036. C.. NATURAL AND PREDACTION RATES COMBINED.
1037. ST=EXP(-AMNAT+PRD))
1038. C.. THE FINAL FINITE RATE IS CALCULATED FOR THE TIME STEP.
1039. AMMORT(1-((ST**C1/CWMN))/DT
1040. GO TO 5
1041. 2 SCASH=EXP(-CASMNT)
1042. SNAT=SCASM**1/2(CASMN)
1043. DUMAM1I(EDUM,PDUM)
1044. xENNAT=SFRAc(OU, SF1, SF2, SF3)
1045. AMNAT=ALOG(X**CWMN)
1046. ST=EXP(-AMNAT+CSMPD))
1047. AMMORT(1-((ST**C1/CWMN))/DT
1048. 5 RETURN
1049. END
1050. C.. FUNCTION AMMORT(IJK)
1051. C.. THIS FUNCTION CALCULATES MORTALITY RATES OF ADULT FEMALES.
1052. INTEGER T,DT,TCON,TPART,GEST,TEND,TSTART,TDEL,T,TA1,TA2,TN1,TN2,
1053. *ALIT.
1054. COMMON/PPOP,OPET(8,400),PREG(8),ALIT(8,400),TSMR(400),USUB(8,400),
1055. *SPOP,FPDP,AGE,TAD(400),PREMOR,CJM,CWM,CASM,DAM(400),DAPD(400),
1056. *DYNR(8,400),DUVR(8,400),INKI,EXP,TPOP,EDU,PDUF,EDUN,PDUM,
1057. *EDU(8),PDUF(8),PDUV(8),SF1, SF2, SF3, CNMN,CMH,MCM,RMF,CFM,CFMR,
1058. *CMNN,CASMNT,CSMPD,CASMN,CJMHAT,CMHPRD,CMRN
1059. COMMON/ND,NS,POD(8),PFR(8),NSH(8),CP1(8),CP2(8),CP3(8),CDP1(8),
1060. *CMNN,CMNN,CASMNT,CSMPD,CASMN,CJMHAT,CMHPRD,CMRN
1061. COMMON/ND,NS,POD(8),PFR(8),NSH(8),CP1(8),CP2(8),CP3(8),CDP1(8),
1062. *CMNN,CMNN,CASMNT,CSMPD,CASMN,CJMHAT,CMHPRD,CMRN
1063. COMMON/ND,NS,POD(8),PFR(8),NSH(8),CP1(8),CP2(8),CP3(8),CDP1(8),
1064. *CMNN,CMNN,CASMNT,CSMPD,CASMN,CJMHAT,CMHPRD,CMRN
1065. COMMON/ND,NS,POD(8),PFR(8),NSH(8),CP1(8),CP2(8),CP3(8),CDP1(8),
1066. *CMNN,CMNN,CASMNT,CSMPD,CASMN,CJMHAT,CMHPRD,CMRN
1067. COMMON/ND,NS,POD(8),PFR(8),NSH(8),CP1(8),CP2(8),CP3(8),CDP1(8),
1068. *CMNN,CMNN,CASMNT,CSMPD,CASMN,CJMHAT,CMHPRD,CMRN
1069. *CMNN,CMNN,CASMNT,CSMPD,CASMN,CJMHAT,CMHPRD,CMRN
1070. C.. INTER AND SUMMER MORTALITY ARE TREATED SEPARATELY.
1071. IF(MON.LE.3,OR,MON.GE.11)GO TO 1
1072. IF(MON.GT.3,AND,MON.LT.11)GO TO 2
1073. 1 PROD=CWMRD
1074. IF(MON.GE.11)PRD=CWMRD
1075. C.. INTERVAL FINITE SURVIVAL IS THE EXPONENTIAL OF INSTANTANEOUS
1076. C.. NATURAL MORTALITY.
1077. SCASH=EXP(-CASMNT)
1078. C.. TIME STEP FINITE SURVIVAL IS DEPENDENT UPON THE LENGTH OF THE LIFE
1079. C.. HISTORY STAGE.
1080. SNAT=SCASM**1/CWMN
1081. C.. NATURAL SURVIVAL IS MODIFIED BY ENERGY AND PROTEIN DEFICIENCY UNITS
1082. DUMAM1I(FDUM,PDUM)
1083. xENNAT=SFRAc(OU, SF1, SF2, SF3)
1084. C.. MODIFIED INSTANTANEOUS NATURAL MORTALITY IS THE NEGATIVE LN OF FINITE
1085. C.. SURVIVAL
1086. AMNAT=ALOG(X**CWMN)
1087. C.. TOTAL FINE MORTALITY RATE IS THE EXPONENTIAL OF THE INSTANTANEOUS
1088. C.. NATURAL AND PREDACTION RATES COMBINED.
1089. ST=EXP(-AMNAT+PRD)
227

1090 C...THE FINAL FINITE RATE IS CALCULATED FOR THE TIME STEP.
1091 AFMORT=(1.-(ST**(1./CMN)))/DT
1092 GO TO 5
1093 2 SCASH=EXP(-CASMNT)
1094 SNAT=CASH*(1./CASMN)
1095 DU=MIN(EDUF,PDUF)
1096 X=SNAT*SFRAC(DU,SF1,SF2,SF3)
1097 AFNAT=ALOG(X**CASMN)
1098 ST=EXP(-(AFNAT+CASMPT))
1099 AFOHRT=(1.-(ST**(1./CASMN)))/DT
1100 5 RETURN
1101 END
1102 C...
1103 C...
1104 FUNCTION SFRAC(DU,SF1,SF2,SF3)
1105 C...THIS FUNCTION MODIFIES SURVIVAL BASED ON NUTRITIONAL DEFICIENCY UNITS.
1106 SFRAC=SF1/(1.+SF2*EXP(-SF3*DU))
1107 RETURN
1108 END
1109 C...
1110 C...
1111 SUBROUTINE POPOUT(DUG,TSTART,TEND,DT,LITMAX,INT)
1112 C...THIS SUBROUTINE OUTPUTS POPULATION DENSITY RESULTS.
1113 4 INTEGER T,DT,ICON,T,M,TAD,OT,LITMAX,TEN
1114 8 ALITS
1115 DIMENSION XX(5I2),YYP(5,52),YYA(5,52),YNP(50)
1116 COMMON/PREG/(8,400),PREG(8,400),TSUR(400),OSUB(8,400),
1117 *SPOP,PPOP,AGE,TAD(400),PREMO,CJM,CWM,CASHM,DAD(400),DADF(400),
1118 *DYNG(8,400),DUX(8,400),AUX(8,400),TDY(8,400),
1119 *EDUY(8),PDUY(8),PDUJ(8),PDUJ(8),SF1,SF2,SF3,CWMNAT,CJMPAO,CJM,
1120 *CWM,CASHM,CASHPD,CASHM,CJMNP,CJMPAO,CJM
1121 IF(DUG.EQ.1.)WRITE(6,'(/)'PREG,TAD,TPROP,
1122 READ(5,/)OUT,IS,IA,MS,HA
1123 WRITE(6,2011)
1124 2011 FORMAT('RESULTS OF SIMULATION==DEMOGRAPHICS')
1125 TEND=TEND+DT
1126 DO 905 J=TSTART,TEND,DT
1127 PERM=DADM(J)/TAD(J)
1128 IF(DUG.EQ.6.)WRITE(6,'(/)'J,PERM
1129 905 CONTINUE
1130 IF(DUG.EQ.101.)GO TO 906
1131 GO TO 37
1132 C...WRITE AND PLOT DENSITY OF ALL SUBADULTS COMBINED
1133 906 CONTINUE
1134 WRITE(6,2004)
1135 DO 901 J=TSTART,TEND,DT
1136 901 WRITE(6,2005)J,(DSUB(J,I),I=1,LITMAX)
1137 INK=TEND/INT
1138 DO 902 J=INK,LITMAX
1139 DO 902 I=1,INK
1140 T=INT
1141 XX(1:INT)
1142 YYP(J,T)=DSUB(J,T)
1143 902 CONTINUE
1144 IF(OUT.EQ.1.)CALL PLTS(LITMAX,INK,XXP,YYP,A)
1145 C...WRITE AND PLOT DENSITY OF ADULTS
1146 WRITE(6,2006)
1147 DO 903 J=TSTART,TEND,DT
1148 903 WRITE(6,2008)J,DADF(J),DADM(J)
1149 DO 904 I=1,INK
1150 T=INT

C**WRITE DENSITY IN SPRING, DENSITY IN FALL AND FALL AGF RATIOS.

1153 YYA(I,J) = TAD(I)
1154 CALL SUBR(T)
1155 IF(OUT,EQ.,1) CALL PLOTS(I,IN,K,XXP,YYA,B)

37 CONTINUE

923 SPUP = TAD(15)
924 FPUP = TAD(15)+SUBR(I)

933 WRITE(6,2010)
934 WRITE (6,2008), SPUP, FPUP, AGE
935 CONTINUE

1162 2004 FORMAT('O', 'DENSITY PER HA OF SUBADULTS BY LITTER IN YEAR', I5)
1163 2005 FORMAT(1'I', 'I4,8X,5(5X,F10,5))
1164 2006 FORMAT(1'I', 'I4,5X,5(10X,F10,5))
1165 2010 FORMAT(I, 'YEAR', 11X, 'SPRING POPN', 9X, 'FALL POPN', 11X, 'PROP ADULT' *
1166 8 IN FALL POPN')
1167 RETURN
1168 END

C** 

C** SUBROUTINE MEAT (HM, T, TEMP, BHP, THP)

C** THIS SUBROUTINE CALCULATES TOTAL HEAT PRODUCTION REQUIREMENTS, BASED

C** ON BODY WEIGHT AND AVERAGE TEMPERATURE.

1175 INTEGER I, D, T, TEND, TSTART, TDEL, TODEL, TDEC, TDIFF, TTH, TDIFF, TTH
1176 REAL HH, MED IET, LACHED, JRATE, NMLK, LINC
1177 COMMON/DT, DT, TSTAHT, TEND, NLIT, NNL, TON(8), TPAR(8)
1178 COMMON/AIO, IPAK, TDEL, LAG, GEST, TA1, TA2, TNA, TAW, TDA, TMA,
1179 TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA,
1180 TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA,
1181 TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA,
1182 TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA,
1183 TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA,
1184 TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA,
1185 TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA,
1186 TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA,
1187 TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA,
1188 TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA, TMA,
1189 IF(T, LT, ITT, OR, GT, ITT) GO TO 2
1190 C** THERMOREGULATORY REQUIREMENTS DETERMINED.
1191 IF(T, TEMP, LT, HP3) HPINC = HP3 - TEMP
1192 IF(HP3, TEMP, LE, HP4) HPINC = HP4
1193 IF(T, TEMP, GT, HP5) HPINC = HP5 + TEMP
1194 GO TO 3
1195 2 IF(T, TEMP, LT, HP6) HPINC = HP6 + PI
1196 IF(HP6, TEMP, AND, LE, HP12) HPINC = HP12
1197 IF(T, TEMP, GT, HP12) HPINC = HP12 + TEMP
1198 3 THPB = HPB * HPINC + BHP * AMI
1199 RETURN
1200 END

C** 

C** SUBROUTINE NUTRAT(DIFT, GE, GEFAT, CP, CPDIET)

C** THIS SUBROUTINE SETS UP NUTRITIONAL MATRICES BASED ON DIARY

C** COMPOSITION, AND PLANT ENERGY AND PROTEIN CONTENT.

1205 INTEGER I, D, T, TCON, TPAR, GEST, TEND, TSTAHT, TDEL
1206 REAL HEM, HEM, LACHED, JRATE, NMLK, LINC
1207 DIMENSION GE(15, 10), CP(15, 10), DIET(15, 10), GEFAT(15), CPDIET(15)
1208 DD 11 J = 1
1210 DD 10 K = 1
1211 ANDIET(J, K) * GE(J, K)
SUBROUTINE FETUS(IT)
C., THIS SUBROUTINE CALCULATES POTENTIAL GROWTH RATES OF FETUSES.
INTEGER T, DT, ICON, TPART, GEST, TEND, TSTART, TLDEL
REAL ME, MPDIET, LFAPRD, JRATE, NEMLK, LINC
COMMON/KFET(400), PFET(8, 400), WYN(8, 400), PWYN(8, 400),
* WJUV(8, 400), PWJUV(8, 400), LITS(8), WADM(400), WADF(400), PXY(8),
* PKJ(8), GF(15, 10), P(15, 10), DIET(15, 10), GEDIET(15, 10), CDIET(15, 10),
* DMP(400), DMP(400), R(8), RATE, DRATE, RATE(8), JRATE(8),
* RDF(8), TOERY(8), FJUVY(8), EY(8), DCP(8), PBV(8), PFDJ(8), TDAERJ(8),
* FDJN(8), EBJ(8), DCPJ(8), PBJ(8), EBM, ERB, EPR, PRF, TONX, TONRF,
* TONRJ(8), TONRJ(8), AV(365, 5), V(365)
COMMON/DTD, DT, TSTART, TEND, NLIT, NNL, MON, ICON(8), TPART(8)
COMMON/AIOP, IBPK, TLDEL, LAG, GEST, TA1, TA2, TWIN1, TWIN2, ICP, IT4, ITS
* ITT, ITT, ICON, LITMAX
COMMON/C/DDY, FMM, HPP, TATPN, HP2, GMLX, CMFX, CNGL, PIP1, PP2, LINC, PNC,
* DIGMCP, ANI, GP2, HPAR, K1, C1, C2, C3, CY, CJ, GAINC, AFN, AFF, ARH, ARF, CORP,
C., NEMLK, RAL, CAT, UE, PCAT, PRMN, AYA, AYB, AYC, AYD, RDA, ROM, RDC, RDD,
* FDIM, FDF, STOP, FBDPE, HP, HPV, HT, HP8, HP10, HP11, HP13, HP14, EFAT,
* EPRO, GPI, GRE, MAX, HP3, HP6, HP9, HP12, HP1, CONA, CONB, CONK, CONL, CONN,
* CONS
IF(NLIT, EQ, 0) GO TO 3
IF(IT, EQ, GEST+DT) GO TO 3
C., CALCULATE RATES
IF(ITL, IT4) FRATE=1
IF(ITL_ LE, IT4, AND, ITL, IT4) FRATE=2
IF(ITL_ LE, IT4, AND, ITL, GEST) FRATE=3
IF(PFET(NLIT, T+DT) * PFET(NLIT, T)) * FRATE
IF(EQ, TLDEL) GO TO 4
RETURN
4 IF(LITS(NLIT), EQ, 1) GO TO 3
C., RATES ARE MODIFIED BY LITTER SIZE,
FRATE=FRATE*(FLOAT(LITS(NLIT))**(-RH))
3 RETURN
END
C.,
C., THIS SUBROUTINE CALCULATES POTENTIAL GROWTH RATES OF YOUNG AND
C., JUVENILES.
INTEGER T, DT, ICON, TPART, GEST, TEND, TSTART, TLDEL
REAL ME, MPDIET, Lavad, JRATE, NEMLK, LINC
DIMENSION (10)
COMMON/KFET(400), PFET(8, 400), WYN(8, 400), PWYN(8, 400),
* WJUV(8, 400), PWJUV(8, 400), LITS(8), WADM(400), WADF(400), PXY(8),
* PKJ(8), GF(15, 10), P(15, 10), DIET(15, 10), GEDIET(15, 10), CDIET(15, 10),
* DMP(400), DMP(400), R(8), RATE, DRATE, RATE(8), JRATE(8),
* RDF(8), TOERY(8), FJUVY(8), EY(8), DCP(8), PBV(8), PFDJ(8), TDAERJ(8),
* FDJN(8), EBJ(8), DCPJ(8), PBJ(8), EBM, ERB, EPR, PRF, TONX, TONRF,
* TONRJ(8), TONRJ(8), AV(365, 5), V(365)
COMMON/DTD, DT, TSTART, TEND, NLIT, NNL, MON, ICON(8), TPART(8)
COMMON/AIOP, IBPK, TLDEL, LAG, GEST, TA1, TA2, TWIN1, TWIN2, ICP, IT4, ITS
* ITT, ITT, ICON, LITMAX
COMMON/C/DDY, FMM, HPP, TATPN, HP2, GMLX, CMFX, CNGL, PIP1, PP2, LINC, PNC,
* DIGMCP, ANI, GP2, HPAR, K1, C1, C2, C3, CY, CJ, GAINC, AFN, AFF, ARH, ARF, CORP,
C., NEMLK, RAL, CAT, UE, PCAT, PRMN, AYA, AYB, AYC, AYD, RDA, ROM, RDC, RDD,
* FDIM, FDF, STOP, FBDPE, HP, HPV, HT, HP8, HP10, HP11, HP13, HP14, EFAT,
* EPRO, GPI, GRE, MAX, HP3, HP6, HP9, HP12, HP1, CONA, CONB, CONK, CONL, CONN,
C., CONS
IF(NLIT, EQ, 0) GO TO 11
DO 2 J=1, NNL
II(J) = II(J)+DT

C.. GROWTH RATE OF YOUNG DETERMINED.
YRATE(J) = CY
IF(II(J), .EQ., DT) GO TO 3
IF(II(J), .GE., 180K) GO TO 10

C.. POTENTIAL BODY WEIGHT CALCULATED FOR COMPARATIVE PURPOSES.
PWYNG(J,T+DT) = PWYNG(J,T)+DT*YRATE(J)
GO TO 2

C.. GROWTH RATE OF JUVENILES DETERMINED.
JRAT(J) = XR*CX*EXP(-CX*FLOAT(II(J)))
IF(JRAT(J), .EQ., 180K) GO TO 4
PJUV(J,T+DT) = PJUV(J,T)+DT*JRAT(J)
GO TO 2

3 PJUV(J,T+DT) = PJUV(J,T)+DT*JRAT(J)
GO TO 2

4 PJUV(J,T+DT) = PJUV(J,T)+DT*JRAT(J)
CONTINUE
DO 11 J=1, NNL
PJY(J) = PJY(J)+YNG(J,T+DT)-YNG(J,T)
PJH(J) = PJH(J)+JUV(J,T+DT)-JUV(J,T)
IF(II(J), .EQ., DT) PJY(J) = PJY(J)+YNG(J,T+DT)
IF(JRAT(J), .EQ., 180K) PJY(J) = PJY(J)+YNG(J,T)
IF(JRAT(J), .EQ., 180K) PJH(J) = PJH(J)+JUV(J,T+DT)
PJY(J) = 0

11 CONTINUE
RETURN
END

C..
C.. THE FUNCTIONS RNOR, RP, AND RI CONSTITUTE THE STOCHASTIC PARAMETER
C.. GENERATOR. FUNCTION RI CONVERTS REAL INPUTS INTO INTEGER TYPE
C.. PARAMETERS AND FUNCTION RR GENERATES REAL TYPE PARAMETERS.
C.. FUNCTION RNOR(IR)
C.. GENERATES A RANDOM NORMAL NUMBER (0,1)
C.. IARG IS A LARGE ODD INTEGER FOR A BEGINNING ARGUMENT
C.. REQUIRES FUNCTION R0 WHICH GENERATES A UNIFORM RANDOM NUMBER 0-1

$SET ON
DATA 1/A/
$RESET ON
IF(1, .GT., 0) GO TO 30
10 X*R*0*RNOR(IR)=1.0
Y*R*0*RNOR(IR)=1.0
S*X*Y*Y
IF(S, .GE., 1.0) GO TO 10
S=SRT(2.0*ALOG(S)/S)
RNOR=R*S
$SET ON
GN2PY=8
$RESET ON
I=1
GO TO 40
30 RNOR=02
I=0
40 RETURN
END

FUNCTION RI(HL,DL,IK)
XR=RNOR(IR)+DL
IF(X, .LT., 0.) A=-5
IF(X, .GE., 0.) A=5
IK=HL*A
RETURN
END

GO TO 2
FUNCTION AR(RP, DP, IR)
*RNQK(IR)*DP
KP*PP+Y
RETURN
END
C..
Appendix C

Nutrient Content Matrices and Dietary Input Matrices
The following are the nutrient content and diet proportion matrices for low population conditions:

<table>
<thead>
<tr>
<th>MONTH</th>
<th>HALOGETON</th>
<th>ARTEMISIA</th>
<th>KOCHIA</th>
<th>FORBS</th>
<th>GRASSES</th>
<th>SARCONATUS</th>
<th>A FALCATA</th>
<th>CHRYSOOTHAMNUS</th>
<th>A CONFERTIFOLIA</th>
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The following are the nutrient content and diet proportion matrices for high population conditions:

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<th>GRASSES</th>
<th>SARCOPHATUS</th>
<th>A FALCATA</th>
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**Dietary Proportions**

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Appendix D

Dietary Data and Data of Crude Protein

Analysis of Kochia Plants
Table D.35. Mean and standard deviations of percentages of plant species in jackrabbit diets in 1976 in Curlew Valley, Utah. Sample sizes are in parentheses.

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<th>Plant species</th>
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<th>Fall (39)</th>
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<td>11.99 ± 19.72</td>
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<td>Atriplex falcata</td>
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<td>0.99 ± 4.11</td>
<td>1.21 ± 3.95</td>
<td>22.10 ± 21.76</td>
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<td>Sarcobatus vermiculatus</td>
<td>52.69 ± 27.68</td>
<td>0.72 ± 3.12</td>
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<tr>
<td>Kochia americana</td>
<td>0.37 ± 0.90</td>
<td>4.92 ± 11.73</td>
<td>1.01 ± 3.80</td>
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<td>Chrysothamnus viscidiflorus</td>
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<td>8.98 ± 12.51</td>
<td>4.35 ± 7.33</td>
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<td>Chrysothamnus nauseosus</td>
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<td>Ceratoides lanata</td>
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<td>Bromus tectorum</td>
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<td>20.36 ± 14.80</td>
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<td>0.04 ± 0.19</td>
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Table D.36. Percentage crude protein of segments of Kochia plants collected in September 1976, in Curlew Valley, Utah.

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<sup>a</sup> Means not significantly different from one another by ANOV (p < .05).
VITA

William Richard Clark
Candidate for the Degree of
DOCTOR OF PHILOSOPHY

Dissertation: Population Limitation of Jackrabbits: An Examination of the Food Hypothesis

Major Field: Wildlife Ecology

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Professional Experience:


Published Articles:

