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A Model of Energy Expenditure in White-Tailed Jackrabbits (*Lepus townsendii*) Based on Integrated Studies of Energetics and Field Ecology

Gordon L. Rogowitz
Utah State University

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A MODEL OF ENERGY EXPENDITURE IN WHITE-TAILED JACKRABBITS (LEPUS TOWNSENDII) BASED ON INTEGRATED STUDIES OF ENERGETICS AND FIELD ECOLOGY

by

Gordon L. Rogowitz

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

of

DOCTOR OF PHILOSOPHY

in

Wildlife Ecology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

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Gordon L. Rogowitz

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ABSTRACT

A Model of Energy Expenditure in White-tailed Jackrabbits (*Lepus townsendii*) Based on Integrated Studies of Energetics and Field Ecology

by

Gordon L. Rogowitz, Doctor of Philosophy

Utah State University, 1988

Major Professor: Dr. Michael L. Wolfe
Department: Fisheries and Wildlife

Field and laboratory studies were conducted to develop a model of energy expenditure in a population of white-tailed jackrabbits (*Lepus townsendii*). Field work in southwestern Wyoming during 1985-87 showed that the breeding season commenced at snowmelt and ceased during late-July drought. Adult females reproduced relatively synchronously and produced a mean of three litters annually. Greatest fetal production occurred in the second litter period. Collections indicated a 1:1 sex ratio, few jackrabbits >2 years-old, and a density of 7 animals/km^2 in the population. Postnatal growth was sigmoidal, culminating in heavier adult females than males. Using radio-telemetry, a circadian rhythm was detected in jackrabbit activity, with movement beginning after sunset and ending by sunrise. Observations showed that season, snow cover, weather, lunar phase, and predators influenced activity. Energetics studies established the pattern of seasonal acclimatization in the jackrabbit. Basal metabolic rate (BMR), pelage thickness, and body temperature increased but overall thermal conductance (C) and the lower critical temperature (LCT) declined from summer to winter. High winds and low air temperatures elevated metabolism interactively and their effects were most pronounced during summer. Metabolic rate declined with incident radiation at T_a < LCT during winter but not during summer. In newborn jackrabbits, body temperature dropped despite increased metabolism at $T_a < 25$ °C. Cold tolerance and homeothermy developed with age. Based on these and published data, a FORTRAN model was written that simulated the energy expenditure of a population of jackrabbits. Metabolizable energy requirements for maintenance, thermoregulation, reproduction, growth, and activity were estimated. The model indicated that most energy ($kJ \cdot kg^{-1} \cdot day^{-1}$) was required by adult females during lactation, adult males at the onset of breeding, and newborn juveniles. Energy expenditures for adult females, adult males, and juveniles were 191, 130, and 224 $MJ \cdot individual^{-1} \cdot km^{-2} \cdot yr^{-1}$, respectively. Total energy expenditure increased with wind and lower air temperature and decreased if juvenile huddling was simulated. The model indicated that the jackrabbit population is not limited by food. Estimated percent consumption of forage energy was 4%, assuming 50% of phytomass was edible, the population density = 100 jackrabbits/km^2, metabolizable energy efficiency = 0.4, and the air was calm.

(170 pages)

CHAPTER I

INTRODUCTION

The interactions between hares (Lepus spp.) and their forage resources in natural habitats are complex. Field studies of snowshoe hares (L. americanus) (Keith and Windberg 1978, Pease et al. 1979, Keith et al. 1984) and mountain hares (L. timidus) (Angerbjörn 1981) suggest that population growth in these herbivores is limited by forage availability. In contrast, simulations indicate that black-tailed jackrabbits (L. californicus) are unlikely to be food or energy limited (Clark and Innis 1982, Harris 1984). Bryant (1981) has suggested that unpalatability of forage rather than total phytomass energy constrains population growth in snowshoe hares. The probability of food limitation is increased when plant palatability declines because the quantity of edible and assimilable forage is reduced (Bryant and Kuropat 1980). Several other factors can influence the availability of edible forage such as plant structure (Crawley 1983) and variation in snow cover (Keith 1983). Effects of these variables on potential food limitation by Lepus spp. have not been evaluated fully.

The present investigation was conducted to estimate (1) the daily and annual energy expenditure of a semi-desert population of white-tailed jackrabbits (L. townsendii) and (2) the amount of energy in above-ground phytomass and in edible forage that jackrabbits consume. Gessaman (1973) has reviewed methods of calculating energy expenditure in free-living animals. Although the doubly-labeled water method is probably the most reliable when its assumptions are met, it estimates energy use only for a 1-2 day period, and is therefore impractical for long-term studies. Also, the method assumes that the animal's diet and post-absorptive state, hence, respiratory quotient, are accurately estimated. This is seldom possible for generalist herbivores such as white-tailed jackrabbits (Flinders and Hansen 1972). I considered empirical modelling to be the best approach to estimating daily and annual energy use by white-tailed jackrabbits. Models based on empirical data tend to be less general but more realistic than those based on theoretical assumptions (Levins 1966). Such models have been used successfully to estimate nutritional and energetic parameters in ungulate species (reviewed by Hudson and White 1985).

The model presented here simulated the energy expenditure of a population of white-tailed jackrabbits. Specific energy requirements of adults and juveniles for maintenance, thermoregulation, activity, growth, and reproduction were simulated to estimate the major causes of high energy use. Total population energy expenditure was compared to energy in the standing crop to estimate the percentage of phytomass energy consumed by jackrabbits. Changes in the amount of phytomass available to jackrabbits and in jackrabbit efficiency of metabolizing vegetation were simulated because much of range forage is inaccessible, unpalatable, or indigestible to herbivores (Bryant and Kuropat 1980, Crawley 1983). Variation in population density was also simulated because jackrabbit density fluctuates markedly (Mohr and Mohr 1936, Kline 1963, Dumke 1973, Schwartz 1973).

The study comprised four phases: (1) Field and laboratory studies were conducted. These were required because data on the biology of white-tailed jackrabbits in western USA are limited. Field studies on the following topics provided data to estimate uses of energy: breeding biology (reproductive energy), growth (production energy), seasonal movement pattern (activity energy), microclimate (maintenance and thermoregulatory energy), and population structure (population energy). Physiological studies were conducted to provide data on seasonal energy use by adult jackrabbits, ontogeny of thermogenesis in juveniles, and complex effects of ambient temperature, wind speed, and radiation on energy expenditure. (2) Empirical equations were derived from these studies and from published data. (3) A population energetics model was written based on the empirical equations. (4) Jackrabbit consumption of phytomass energy was evaluated.

CHAPTER II

FIELD-STUDY AREA

An undeveloped area in southwestern Wyoming was chosen for study (Fig. 1). The semi-desert area is part of the western intermountain sagebrush steppe ecosystem described by West (1983). The elevation range is 2000-2400 m. Drought occurs mid-summer and can be ameliorated by rainfall at the end of the growing season. Most precipitation occurs in winter and early spring (National Weather Service data summarized by West [1983]).

Mean annual rainfall was 23.9 cm and mean air temperature 4 °C in southwestern Wyoming, west of the Green River, during 1931-86 (NOAA 1986). Mean incident radiation (direct and diffuse) was approximately 450 W/m^2 and 250 W/m^2 and maximum irradiation level was 1100 W/m^2 and 650 W/m^2 during summer and winter days, 1983, respectively, at Kemmerer, Wyoming (Anon 1984).

VEGETATION

Sagebrush (_Artemesia tridentata_ ssp.) and bunchgrasses dominated the study area. These were relatively equally inter-mixed, however, large areas devoid of shrubs occurred. Plant cover was sparse throughout the area (estimated visually at approximately 60% bare ground). Plant species richness was low but enhanced by the presence of species associated primarily with disturbed roadside habitats.

Grasses on the area included tall wheatgrass (_Elymus lanceolatus_), indian ricegrass (_Oryzopsis hymenoides_), squirreltail (_Elymus elymoides_), needle-and-thread (_Stipa comata_), sandberg bluegrass (_Poa_

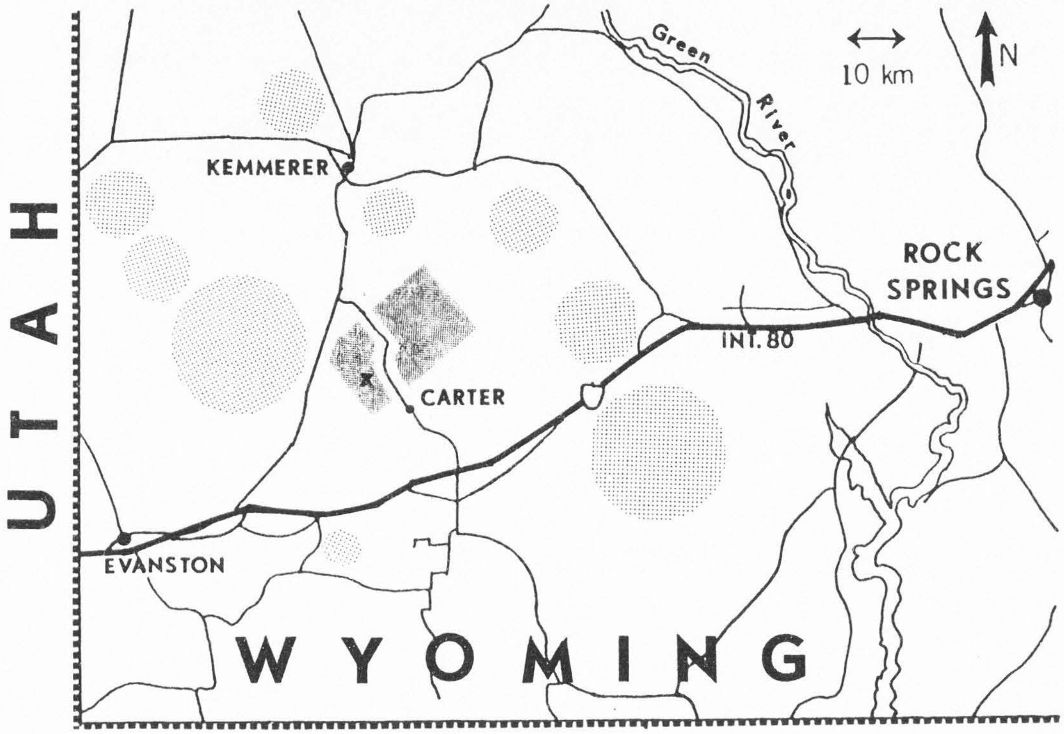

Fig. 1. Study area in southwestern Wyoming. Light hatching indicates locations where jackrabbits were collected (see Chapters III and IV). Dark hatching indicates the area of transects for jackrabbit density estimates (see Chapter IV). The "X" at 10 km NW of Carter designates the site where grass samples were harvested (see Chapter III).

secunda), great basin wildrye (Leymus cinereus), foxtail barley (Critesion jubatum), and cheatgrass (Bromus tectorum). The recent nomenclature for perennial Triticeae follows revisions proposed by Barkworth and Dewey (1985).

Forbs included wild buckwheat (Eriogonum sp.), aster (Aster sp.), phlox (Phlox sp.), pussytoes (Antennaria sp.), astragalus (Astragalus sp.), cryptantha (Cryptantha sp.), owl clover (Orthocarpus sp.) mountain bluebell (Mertensia sp.), penstemon (Penstemon sp.), rubberweed (Hymenoxys sp.), leafy spurge (Euphorbia sp.), Russian thistle (Salsola kali), and halogeton (Halogeton glomeratus).

In addition to sagebrush, major shrubs were shadscale (Atriplex confertifolia), saltsage (A. gardneri), winterfat (Ceratoides lanata), rubber rabbitbrush (Chrysothamnus nauseosus), douglas rabbitbrush (C. viscidiflorus), spineless horsebrush (Tetradymia canescens), and broom snakeweed (Xanthocephalum sarothrae). Small patches of trees on the area, principally of Utah juniper (Juniperus osteospermia), were apparently not used by white-tailed jackrabbits, as indicated by the absence of fecal pellets. visible corpora lutea and unstriated uteri without developing fetuses (n = 56) and the males had testes weights <2 g (n = 34).

CHAPTER III

JACKRABBIT REPRODUCTIVE PATTERN

Analysis of reproductive tracts showed that the breeding season of white-tailed jackrabbits commenced between late February and mid-March and ceased by late July. Dates of first litter conceptions coincided with reduced snow cover but could not be related to monthly air temperature. Adult females produced an average of three litters annually and reproduced relatively synchronously. Conceptions occurred immediately post-partum. All adult females were pregnant in the first two litter periods of the breeding season and a mean of 7 ova/female was produced per litter. Intrauterine loss was higher in the first (mean = 35-39%) than in the second litter period (mean = 5-9%). Most fetuses were produced in the second litter period. During the third litter period, fewer females were pregnant and the pregnant females shed fewer ova (mean = 5-6 ova/female) and had more intrauterine loss (mean = 16-57%) than in litter period two. Testicular mass and the perirenal fat index also declined between the second and third litter periods. Reproductive cessation occurred during summer drought, when the water content of grasses on jackrabbit range was low (26%).

INTRODUCTION

Temperate zone mammals have evolved a pattern of breeding during the period of the year when resources are usually the least limiting (reviewed by Sadleir 1969, Flowerdew 1987). Lepus species conform to this pattern by producing multiple litters in the breeding season via post-partum reproduction (see Flux 1981). In general, fewer litters are produced per season in Lepus species at higher latitudes and elevations, where the growing season is shorter (Flux 1981, Keith 1981, Swihart 1984). At the onset of the breeding season, increasing photoperiod induces hormonal activity leading to sexual receptivity (Bissonnette and Csech 1939, Lyman 1943, Davis and Meyer 1972). Proximate environmental cues may fine tune the breeding onset to coincide with the growing season (Myers and Poole 1962, Conoway and Wight 1962, Meslow and Keith 1971). Conceptions may not always be accurately timed to the onset of favorable conditions. Late-winter storms may induce partial litter resorption during the first litter of the breeding season (Bronson and Tiemeier 1958, Lechleitener 1959, Tiemeier 1965, Flux 1970).

Several environmental variables may influence offspring production (Sadleir 1969). Low nutrient availability in vegetation may decrease ova production and increase intrauterine loss (Sadleir 1972, Widdowson 1981). Low forage water content is associated with reduced litter size and number (Stodart and Myers 1966) and capacity for lactation (Richards 1979).

Because reproductive data are lacking for white-tailed jackrabbits on western range, where summer drought occurs annually (West 1983), the present study was conducted to describe reproduction in a population of white-tailed jackrabbits (Lepus townsendii) in semi-desert habitat in Wyoming. The objectives of this study were to (1) determine the reproductive potential of jackrabbits by examining litter size and intrauterine loss and (2) evaluate effects of climate on the onset and cessation of reproduction.

METHODS

White-tailed jackrabbits were collected in southwest Wyoming during 1985-88 (Fig. 1). The collections were timed to coincide with late pregnancy to detect litter resorption, which occurs chiefly during the first half of pregnancy in *Lepus* spp. (Newson 1964, Flux 1970). Since jackrabbits reproduce synchronously (Kline 1963, James and Seabloom 1969a), the correct date to collect a first-litter sample could be estimated from the ages of fetuses in an early-season collection. Collection dates for subsequent litters could be estimated from previous litter parturition dates because jackrabbits also reproduce during a post-partum heat (Kline 1963, James and Seabloom 1969a).

Jackrabbit reproductive tracts were examined with methods similar to those reported by Gross et al. (1974). Testes were stripped of epididymis and weighed as pairs (± 0.5 g). Ovaries were sectioned laterally and their corpora lutea were counted to estimate the number of ova produced per female per litter. Fetuses were counted *in utero*, removed from the amnion, and weighed to ± 0.1 g. Viable fetuses were considered to be those having morphological characteristics consistent with those expected for their weight (Bookhout 1964). Fetuses that were being resorbed during late pregnancy were identified as pigmented zones or lumps on the uterine horns, usually smaller than viable fetuses in the litter. In this study, litter size refers to the number of viable fetuses found in a litter during late pregnancy.

Intrauterine loss per female jackrabbit per litter, the sum of preimplantation and postimplantation losses, was estimated based on methods described by Lechleitener (1959), where preimplantation loss equals the number of corpora lutea minus the number of visible implantation sites and postimplantation loss (resorption) equals the number of implantation sites minus the number of viable fetuses. Intrauterine loss was expressed as a percentage of the corpora lutea produced.

The breeding season was defined as the period between the dates of first conception and last parturition (French et al. 1965). Conception dates were found by backdating from fetal age which was estimated from the age-specific weight and morphology of snowshoe hares (Bookhout 1964), as described by James and Seabloom (1969a). Parturition dates were estimated by adding the gestation period of white-tailed jackrabbits, approximately 42 days (Kline 1963), to conception dates.

Ages of collected jackrabbits were estimated from their dry lens mass (James and Seabloom 1969b). Methods of eye collection and preservation suggested by Gross et al. (1974) were used to increase precision in age estimates. Jackrabbits >6.5 months-old were assumed to be adults. Most adult jackrabbits were collected during the breeding season following their year of birth.

The perirenal fat content of jackrabbits was examined to index body tissue catabolism during summer drought. As in other Lepus species (Flux 1971), white-tailed jackrabbits store most fat adjacent to the kidney. Similar to criteria used by Chapman et al. (1977), perirenal fat was indexed as 0 = no visible fat, 1 = slight fat restricted to perirenal region, 2 = perirenal fat extends anteriorly along peritoneum, 3 = copious dorsal fat.

Forage water content was estimated during the breeding season of 1986 because vegetation was observed to dry out near the end of the breeding season during 1985. Grass was clipped on 25 plots (area = 0.25 m^2) that were spaced 0.2 km apart on a north-south transect, 10 km northwest of Carter, Uinta County, Wyoming (Fig. 1). Each grass sample was weighed when harvested (wet), dried at 60 °C, and reweighed until further drying had no effect on the sample mass. Forage water content was estimated as (wet mass - dry mass)·100/wet mass.

Snow depth data were compiled from monthly climatological reports (NOAA 1985-87) for Rock Springs, Wyoming. Air temperature was recorded continuously at 0.2 m above ground level at Carter and at 10 km northwest of Carter, Wyoming, using thermographs calibrated to ± 1 °C and placed in ventilated shelters. Thermograph charts were read at 2-hr intervals and the daily means and standard errors were computed. Since temperatures at both locations were similar ($\underline{P} > 0.5$), only Carter data are shown.

RESULTS

The breeding season lasted approximately 141 days in 1985 (6 March to 25 July) and 147 days in 1986 (25 Feb to 22 July). Reproductive females produced an average of three litters annually. Conceptions were relatively synchronous, usually occurring within a 2-week interval during each litter period (Fig. 2). Post-partum breeding occurred immediately following previous parturitions (Table 1).

First litter conception dates were on average two-weeks later in 1985 than in 1986 or 1987 (Table 1). The later conception in 1985 coincided with greater January-February snow accumulation than in 1986

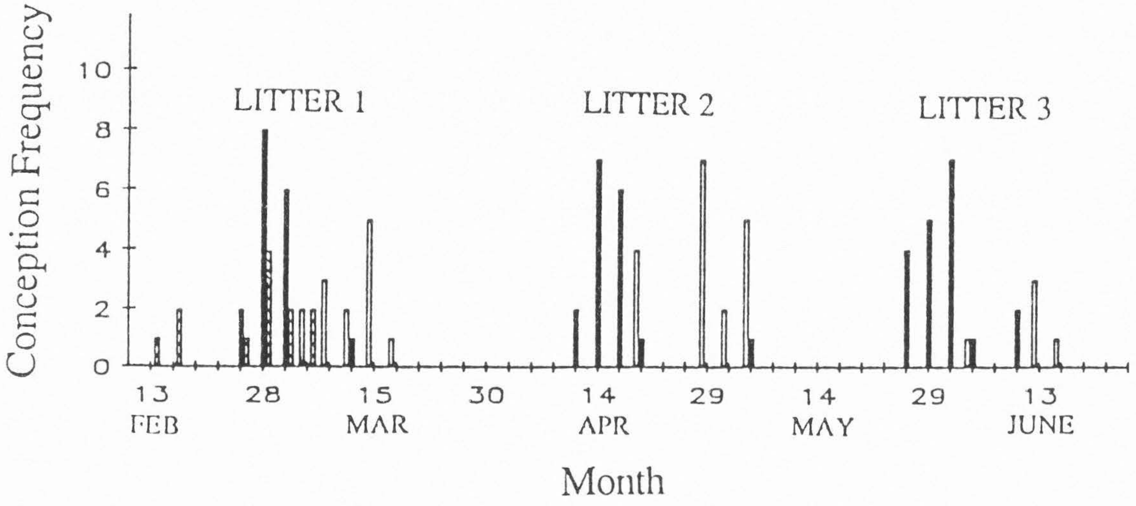

Fig. 2. Conception dates of litters of reproductive female jackrabbits collected in Wyoming, 1985-87 (1985 [open bars]; 1986 [solid bars]; 1987 [hatched bars]). Bar interval width is 3 days (bars are drawn on interval midpoints).

Table 1. Reproductive summary for adult female jackrabbits. Mean dates of conception and parturition, number of ova, number of implanted and viable fetuses, and percent intrauterine loss are reported (SE in parenthesis, range in brackets). Number of breeding females and the total collected (in braces) are designated by n.

	Conception	Parturition	Number Ova	Number Implanted	Number Fetuses	% Loss	n
Litter 1							
	13 Mar 85 [6-19]	25 Apr 85 [17-30]	6.8 (0.3) [4-9]	4.3 (0.4) [3-6]	4.3 (0.4) [3-6]	35 (6) [0-57]	13 {13}
	27 Feb 86 [25-11 Mar]	11 Apr 86 [9-23]	7.1 (0.3) [4-9]	4.5 (0.3) [3-6]	4.5 (0.3) [3-6]	36 (4) [0-57]	17 {17}
	28 Feb 87 [13-7 Mar]	12 Apr 87 [7-25]	6.9 (0.4) [5-9]	4.2 (0.3) [3-6]	4.2 (0.3) [3-6]	39 (4) [0-57]	12 {12}
Litter 2							
	29 Apr 85 [21-6 May]	11 Jun 85 [2-17]	6.6 (0.3) [5-8]	6.3 (0.2) [4-8]	6.2 (0.2) [4-8]	5 (2) [0-20]	18 {18}
	15 Apr 86 [10-19]	28 May 86 [23-1 Jun]	6.8 (0.2) [5-9]	6.2 (0.3) [4-9]	6.2 (0.3) [4-9]	9 (3) [0-43]	17 {17}
Litter 3							
	12 Jun 85 [5-17]	25 Jul 85 [17-29]	6.0 (1.0) [5-7]	4.5 (1.5) [2-5]	3.5 (0.5) [2-5]	57 (8) [40-86]	5 {22}
	31 May 86 [26-9 Jun]	13 Jul 86 [8-22]	5.3 (0.3) [3-8]	4.2 (0.3) [3-7]	4.1 (0.3) [3-7]	16 (5) [0-62]	20 {27}

or 1987 (Fig. 3). Mean conception dates occurred at approximately the commencement of the snow-free period in 1985 (17 March) and 1986 (17 February). Jackrabbits conceived in 1987 while snow was 0 to 8 cm deep.

No clear relationship between the later breeding in 1985, relative to 1986 or 1987, and air temperature could be detected. January air temperatures were lower ($P = 0.003$) in 1985 (-7 ± 0.9 °C; mean ± SE) than in 1986 (0 ± 1.6 °C), but similar ($P = 0.1$) between 1985 and 1987 (-9 ± 0.9 °C). February air temperatures were similar ($P = 0.7$) between 1985 (-6 ± 1.1 °C) and 1986 (-7 ± 1.2 °C) and similar ($P = 0.1$) between 1985 and 1987 (-4 ± 0.5 °C). Air temperatures in January ($P < 0.001$) and February ($P = 0.04$) differed between 1986 and 1987 but mean conception dates were alike during those years (Table 1).

All adult females were pregnant in the first litter period but intrauterine loss averaged 35-39% (Table 1). The intrauterine loss was attributed to preimplantation loss; no postimplantation loss was detected. The greatest fetal production (percentage of reproductive females in collections times the litter size) occurred during the second litter period because all females were pregnant and the litter size was the largest during the breeding season. Only a fraction of females were pregnant in the third litter period. The pregnant females in the third litter period produced an average of 5-6 ova/female, whereas an average of 7 ova/female was produced in earlier litters. The average size of third litters was also smaller and the intrauterine loss was higher than in the second litter. Non-pregnant females collected in the third litter period had small-sized uteri and ovaries, relative to

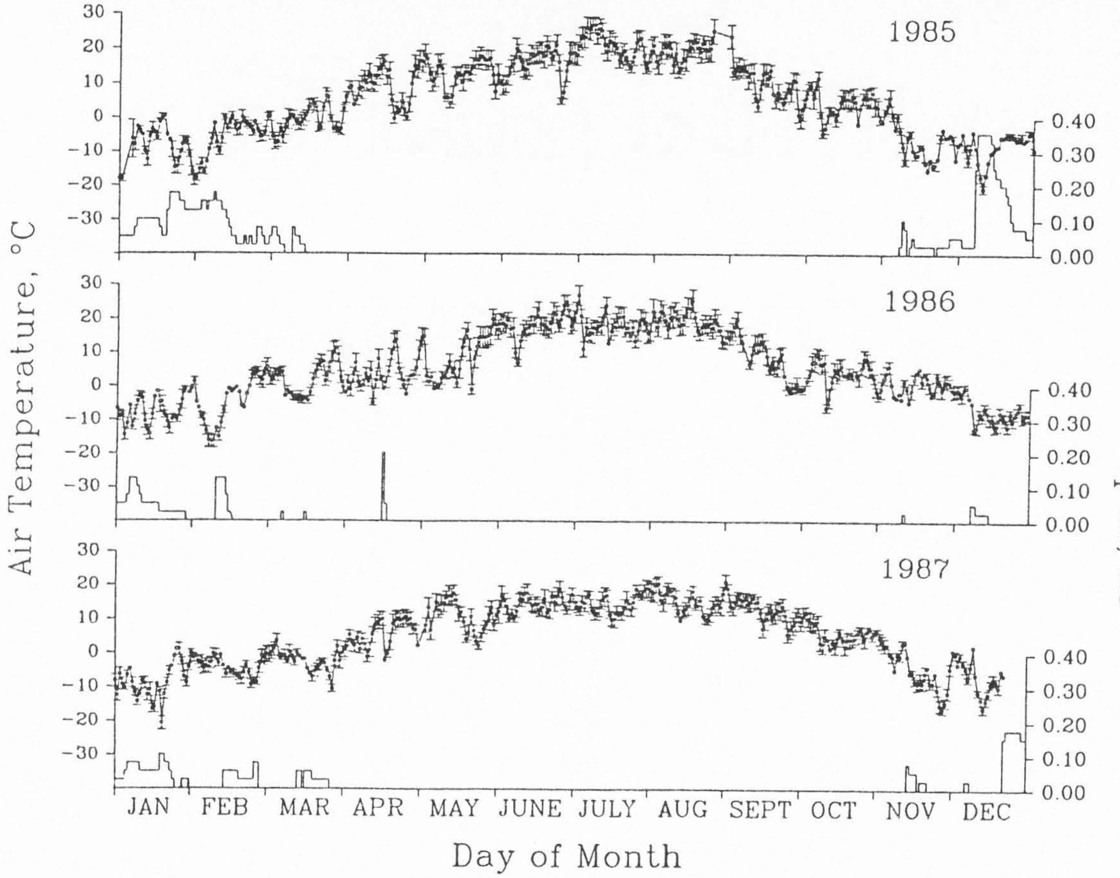

Fig. 3. Daily air temperature (mean ± SE) measured at 0.2 m above ground level at Carter, Wyoming, and snowdepth (indicated by histograms) from monthly climatological data for Rock Springs, Wyoming.

pregnant females, and no visible corpora lutea. However, these females were previously reproductive because they had striated uteri and visible corpora albicantia.

Testes mass and litter size were lower during the last litter period than during the rest of the breeding season (Fig. 4). By the end of July, the testes were fully regressed and no pregnant females were found in jackrabbits collections. This decline in reproduction coincided with lower water content in grasses and a lower perirenal fat index (Fig. 4). The water content fell from 60 ± 0.8% in late April to 26 ± 1.0% in late July, 1986. The perirenal fat index of adults also reached a minima at the breeding season end, 1986. Decline in fat index was most marked in adult females.

Jackrabbits collected during the breeding season in which they were born were non-reproductive: males had testes masses <2 g and females had ovaries with no visible corpora lutea and unstriated fetuses without developing fetuses. The fat index of juvenile jackrabbits collected during June-August (2-4 months-old) was 0.22 ± 0.08 (mean ± SE, $\underline{n} = 45$). The index was higher, 1.21 ± 0.26 ($\underline{n} = 14$), in jackrabbits collected during November (4-7 months-old).

DISCUSSION

The pattern of reproduction found in white-tailed jackrabbits in Wyoming is similar to that of other Lepus species in the temperate zone (Flux 1981) because (1) jackrabbit reproduction was synchronous and occurred immediately post-partum and (2) the breeding season coincided with the more favorable portion of year. Breeding commenced at the late-winter snowmelt and ended prior to the late-summer drought.

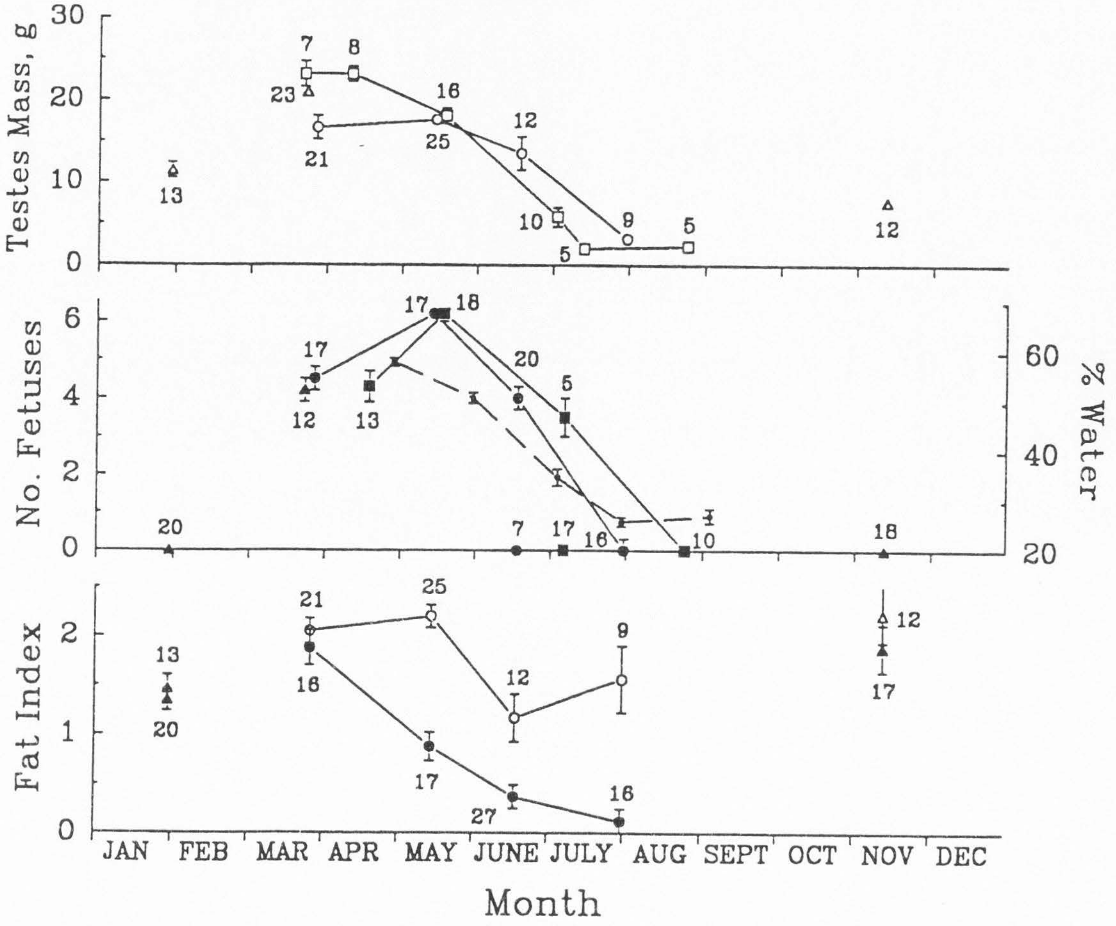

Fig. 4. Seasonal changes in testes mass (mean ± SE), number of viable fetuses, and perirenal fat content of white-tailed jackrabbits and decline in water content of grasses (dashed line). Results for male (open symbols) and female (closed symbols) jackrabbits are reported. Means for 1985, 1986 and 1987 are represented by squares, circles, and triangles, respectively. Sample sizes are shown (_n_ = 25 for grass samples).

White-tailed jackrabbits produced an average of three litters annually in Wyoming. However, a forth litter is produced by white-tailed jackrabbits in North Dakota (James and Seabloom 1969a). The forth litter is conceived in mid-July, a time when drought is apparently too severe to produce a litter in southwest Wyoming.

Onset of Breeding

Of the two climatic variables studied, air temperature and snow cover, only the latter was associated with delayed reproductive onset in white-tailed jackrabbits. Several field studies of North American _Lepus_ species indicate that snow accumulation or lower air temperatures may inhibit the onset of reproduction. Breeding of snowshoe hares (_L. americanus_) in Utah (Clark 1973) and Wisconsin (Kuvlevsky and Keith 1983) (_Lepus americanus_) commences with snowmelt and spring conditions. In snowshoe hares in Alberta, Canada, reproductive onset corresponds with the beginning of the snow-free period, as air temperatures increase (Cary and Keith 1979). However, in a previous study of snowshoe hares in Alberta (Meslow and Keith 1971), a correlation of air temperature or snow cover with breeding onset could not be detected. In white-tailed jackrabbits in Iowa (Kline 1963) and North Dakota (James and Seabloom 1969a), delayed reproduction is associated with winters with heavy snow accumulation and extreme cold. The breeding season of black-tailed jackrabbits (_L. californicus_) in Idaho begins later in years with heavy winter or spring precipitation, whereas air temperature effects are not consistent between years (French et al. 1965).

Determining which factors stimulate or inhibit breeding is complex in field situations (Meslow and Keith 1971). However, the independent studies described above indicate that (1) presence of snow cover is usually associated with delayed onset and (2) low air temperature is not consistently associated with reproductive delay. This suggests that air temperature is less important than snow cover in regulating reproductive onset. Similarly, in experimental studies of snowshoe hare, Lyman (1943) demonstrated that air temperature has no measurable effect on gonadal recrudescence.

Reproduction

The smallest litter sizes of Wyoming jackrabbits occurred during the first and third litters of the breeding season. The size of the first litter was reduced by intrauterine loss, mean = 35-39% (Table 1). This amount of intrauterine loss is common over the jackrabbit's range. The average intrauterine loss is 33-41% in North Dakota (James and Seabloom 1969a) and 40% in Iowa (Kline 1963). Preimplantation loss explained all of first litter intrauterine loss in Wyoming (this study) and 94% in North Dakota (James and Seabloom 1969a).

First litter intrauterine loss might be induced by adverse weather during late winter (James and Seabloom 1969a). Several studies indicate that partial resorption of first litters increases during winter storms (Bronson and Tiemeier 1958, Lechleitener 1959, Tiemeier 1965, Flux 1970). However, this hypothesis is not supported by my study because the majority of first conceptions occurred after the winter storm season, when snow cover had melted. Also, no resorption was detected during the first litter. Perhaps low forage quality in late winter caused the preimplantation loss. Malnutrition reduces litter size in rabbits (Sadleir 1972) and other mammals (Widdowson 1981).

Fetal production was greatest during the second litter period, which suggests that environmental conditions were most optimal during the middle of the breeding season. Reproductive success declined between the second and third litters because fewer females were pregnant and the litter sizes of pregnant females decreased. White-tailed jackrabbits in North Dakota have a similar, but later, reduction in fetal production at the end of the breeding season (James and Seabloom 1969a), perhaps because conditions there remain mesic later in the year. Lower fetal production in the last litter of the season also occurs in populations of black-tailed jackrabbits in Idaho (French et al. 1965) and Utah (Gross et al. 1974).

Water depletion may have caused the reduction in fetal production and subsequent reproductive cessation in jackrabbits. Free water was not available on arid lands during my study and the water content in grasses declined to 26% at the end of the breeding season, which is less than half of the forage water requirement for black-tailed jackrabbits, 65% (Nagy et al. 1976). Because body tissue is catabolized by wild rabbits (Oryctolagus cunniculus) when available water declines (Cooke 1982a,b), increased catabolism at the end of the breeding season might have lowered the fat index and production of fetuses in white-tailed jackrabbits. Lactating females and juveniles, which have the highest water turnover rates in rabbits (Richards 1979), may be the most susceptible to drought. Reproductive females and juveniles retained the least perirenal fat during the dry season.

CHAPTER IV

JACKRABBIT GROWTH AND POPULATION STRUCTURE

The average density of white-tailed jackrabbits studied in southwestern Wyoming was 7 animals/km^2 during 1985-87. The sex ratio did not differ significantly from 1:1. Fewer than 1% of jackrabbits in collections were >2 years-old and the modal age of adults was 8 months-old. Adult body mass varied seasonally, with females weighing most during the breeding season and males weighing most in autumn. Adult females weighed more than adult males in all seasons except autumn. The average growth rate varied from 18-27 g/day in captive jackrabbits between 25 and 100 days-old. Postnatal growth was described by fitting von Bertalanffy, logistic, and Gompertz curves to age-specific body masses of captive and wild jackrabbits. Each sigmoidal curve explained >90% of the variance in body mass but the logistic and Gompertz curves consistently underestimated birth mass.

INTRODUCTION

Most of the available information on the demography and growth of white-tailed jackrabbits (Lepus townsendii) is from populations located east of the Rocky Mountains, which comprise a different subspecies (L t. campanius) than western jackrabbits (L. t. townsendii) (Hall 1981). In the easterly populations, the density of jackrabbits varies annually (Mohr and Mohr 1936, Kline 1963, Dumke 1973, Schwartz 1973). The sex ratio, estimated in Iowa, approximates 1:1 (Kline 1963). The body mass of adults varies seasonally and females weigh more than males (Kline 1963, Bear and Hansen 1966, James and Seabloom 1969b). Growth and age data have not been described for wild white-tailed jackrabbits. However, a growth curve is available for hand-fed jackrabbits (Bear and Hansen 1966).

Because data from eastern regions may not apply to western populations and reliable data were required for the energetics model (Chapter IX), I conducted a field study of white-tailed jackrabbits in Wyoming during 1985-87. The study objectives were to describe the population density, sex ratio, adult age structure, seasonal variation in body mass, and pattern of lifespan growth.

METHODS

The density of white-tailed jackrabbit was estimated on an a 310 km^2 area in southwestern Wyoming (Fig. 1) with the line transect method of Burnham et al. (1980). Use of this method to estimate jackrabbit density is described by Smith and Nydegger (1985). Two people spotlighted jackrabbits from a vehicle driven 24 km/hr on unpaved roads. The roads were driven from dusk until dawn during mid-March and mid-October. The perpendicular distance of each jackrabbit from the center of the road was recorded. The population density was then computed using the Fourier series estimator in program TRANSECT (Burnham et al. 1980).

White-tailed jackrabbits were collected at sites other than those designated for population density estimation (Fig. 1). Jackrabbits were weighed (± 0.02 kg) immediately upon collection. Reproductive tracts were examined to verify sex. Methods recommended by Gross et al. (1974) were used to collect and preserve the eye. The age of each jackrabbit was then estimated by determining its age class from its dry lens mass

(James and Seabloom (1969b) and assigning age as the midpoint of that age class. Sex ratios were calculated for young of the year (animals collected in the breeding season in which they were born) and adults. A jackrabbits that was >6.5 months-old was assumed to be an adult. Most adult jackrabbits were collected during the breeding season following their year of birth.

A captive population of white-tailed jackrabbits was maintained at the Green Canyon Ecology Compound, Utah State University, Logan, Utah. This was necessary because a sufficiently large sample of body masses of young jackrabbits could not be obtained in Wyoming. A sample of 60 body masses of 4 to 153 day-old jackrabbits was obtained from ten offspring born to three captive females in April and June, 1987. Lactating females and weaned jackrabbits were supplied ad lib. with commercial rabbit chow, apples, and alfalfa.

Growth curves were derived from age-specific body masses of wild and captive, non-reproductive jackrabbits. I used the simplex algorithm for non-linear estimation (Caceci and Cacheris 1984) to fit the Gompertz, logistic, and von Bertalanffy growth equations (Zullinger et al. 1984) to the data. Predicted body masses were regressed on actual body masses to estimate the variance explained by each fitted curve.

RESULTS

Jackrabbit density did not vary between seasons or years (Table 2). The mean density was 7 jackrabbits/km^2 during 1985-87. A total of 358 adults and 91 young of the year were collected. Neither the sex ratio

Table 2. Population density of white-tailed jackrabbits (animals/km^2) estimated with program TRANSECT (Burnham et al. 1980). Lower (LCL) and upper (UCL) 95% confidence limits, sample size (*n*), and total road length of transects (km) are reported.

Date	Point Estimate	LCL	UCL	*n*	km
1985					
March	7.0	4.4	9.5	41	47
October	7.2	4.8	9.6	45	76
1986					
March	6.2	1.6	10.9	15	64
October	6.4	3.8	9.1	43	61
1987					
March	6.4	4.3	8.4	47	63
October	9.0	6.3	11.8	69	68

of adults nor young of the year differed from 1:1 ($\underline{X}^2$, $\underline{P} > 0.5$). The male:female ratio was 1.0:1.2 for adults and 1.0:1.0 for young of the year.

Age distributions were constructed for adults collected during late February to late July (Fig. 5). The modal age for both males and females was 8 months-old. The distributions were skewed towards older age. Fewer than 1% of the collected jackrabbits were >2 years-old.

Adult jackrabbits varied seasonally in body mass (Fig. 6). Females weighed most during the breeding season; males weighed most in autumn. The greatest overlap between sexes occurred in mid-October. Although sexual dimorphism in body mass was most apparent during spring and summer (Fig. 6), the body mass of females (2.93 ± 0.03 kg [mean ± SE]) was also higher than that of males (2.79 ± 0.04 kg) during winter, November-January ($\underline{t} = 3.0$, $\underline{P} = 0.004$, $\underline{df} = 61$). I tested for sex-specific differences in body mass at 50 day increments up to 500 days of age because juveniles appeared to have less dimorphism than adults. A difference in body mass between sexes was detected only in jackrabbits that were >150 days old ($\underline{t} = 4.7$, $\underline{P} < 0.001$, df = 114).

The mean postnatal growth rate varied from 18-27 g/day in captive jackrabbits during the period between 25 and 100 days-old (when growth appeared to be linear; Fig. 7). Reduced growth rate may have occurred in larger litters but the sample size was insufficient to test this hypothesis. The body mass (M) of the captive jackrabbits was expressed as a function of their age in the following regression:

$$M_{kg} = 0.0143 - 0.0186 \cdot AGE_{days} \quad (\underline{r} = 0.935).$$

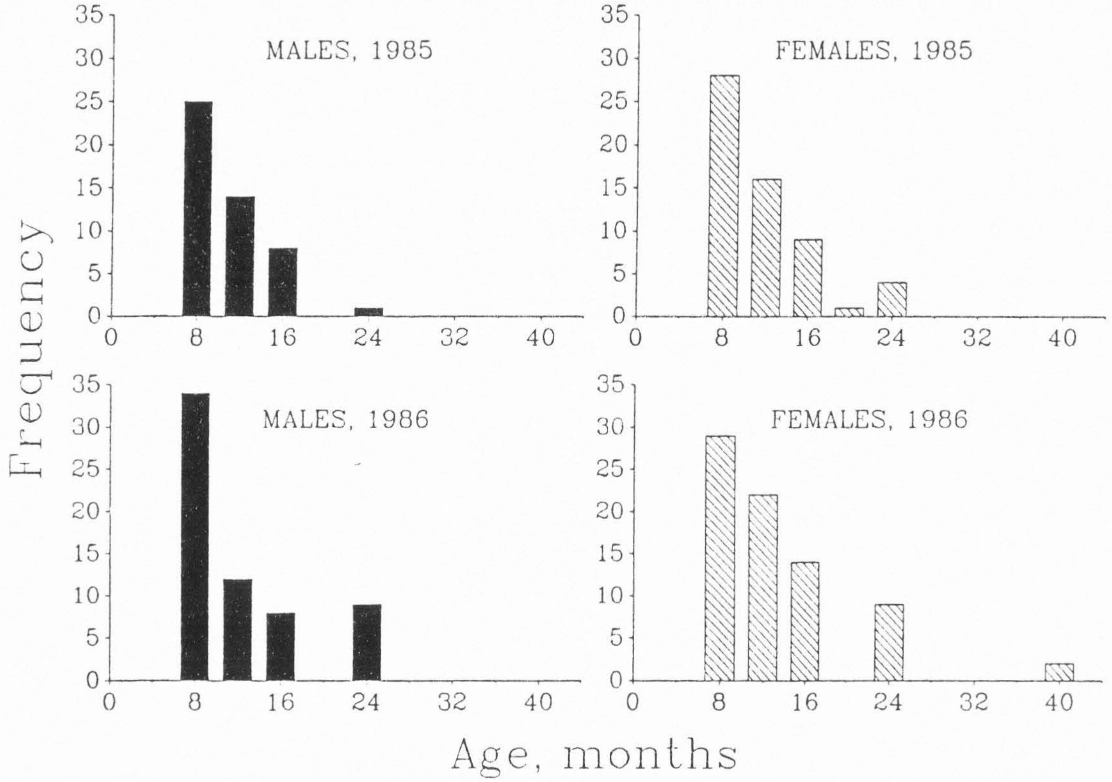

Fig. 5. Age distributions of adult white-tailed jackrabbits collected during the breeding season (frequency = number of animals).

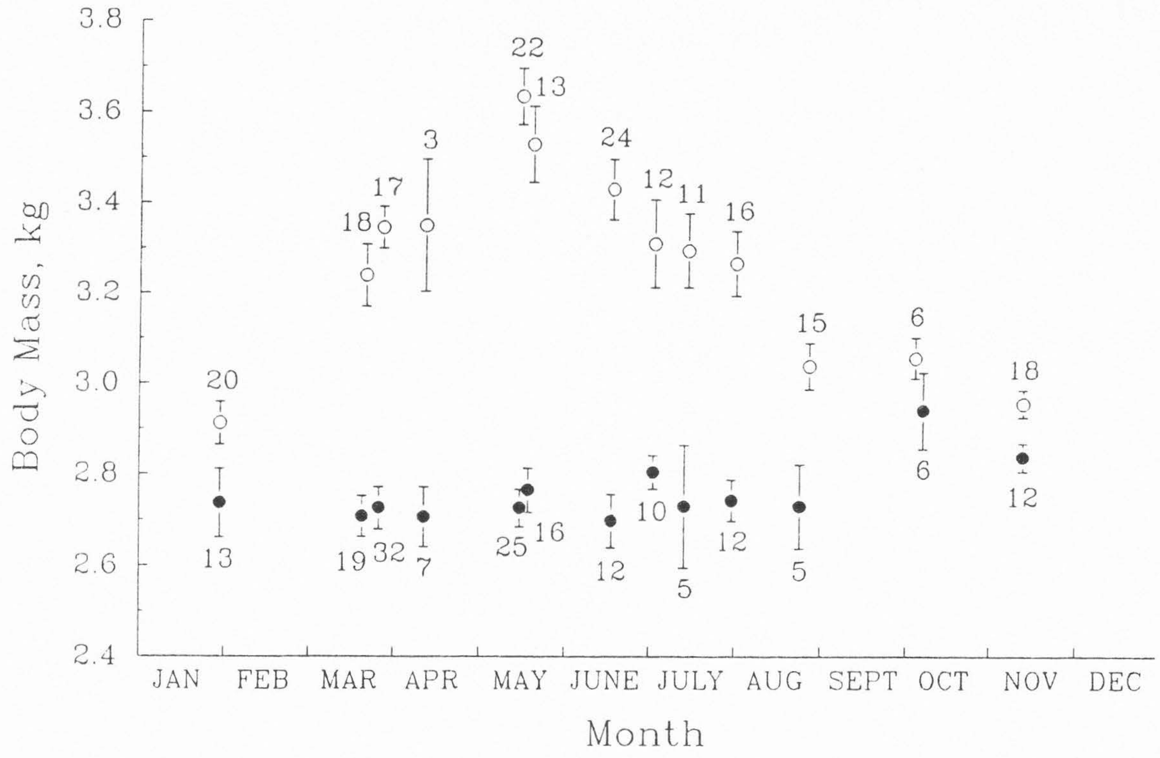

Fig. 6. Seasonal changes in body masses (mean ± SE) of adult female (open circles) and male (solid circles) white-tailed jackrabbits. Numbers designate the sample sizes.

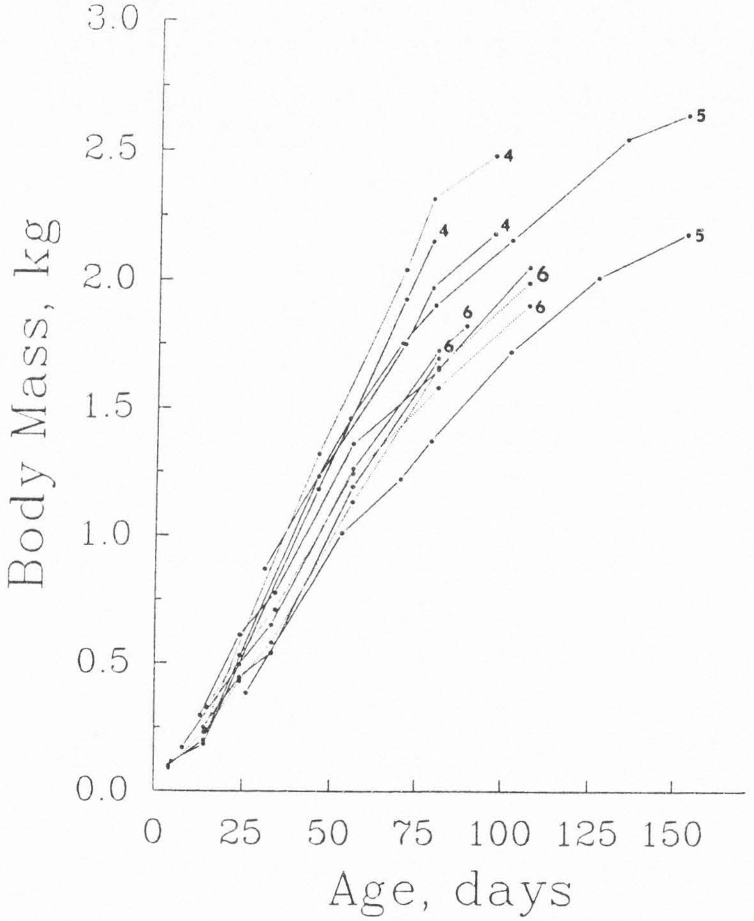

Fig. 7. Early growth of captive male (solid lines) and female (dotted lines) white-tailed jackrabbits fed <u>ad lib</u>. Numbers indicate sizes of litters for respective curves.

Von Bertalanffy, Gompertz, and logistic curves were fit to the age-specific body masses of captive and wild white-tailed jackrabbits (Fig. 8). Each sigmoid curve explained approximately 90% of the variance in body mass (Table 3). The von Bertalanffy and Gompertz curves gave similar estimates of the growth rate constant, inflection point, and asymptotic body mass. The logistic curve predicted a later inflection point, a higher growth rate constant, and a lower asymptotic body mass relative to the other curves.

The most apparent difference between curves was in predicted birth mass. Full-term fetuses of white-tailed jackrabbits weighed 87-115 g (_n_ = 5) in Wyoming (this study) and 84-93 g (_n_= 6) in Colorado (Bear and Hansen 1966). The von Bertalanffy curves estimated actual birth mass much more closely than did the Gompertz or logistic curves (Table 3). Male and female growth data were fit separately with the von Bertalanffy curve (Fig. 8, inset).

DISCUSSION

Harvest and abundance indices indicate that white-tailed jackrabbit populations vary significantly between years (Dumke 1973, Schwartz 1973). A peak density of 27-32 jackrabbits/km^2 occurs in Minnesota but a density of 4-8 jackrabbits/km^2 is more typical (Mohr and Mohr 1936). The density also varies in Iowa, where 11 jackrabbits/km^2 is high relative to usual densities (Kline 1963). The estimated density on my study site, 7 jackrabbits/km^2 during 1985-87, was intermediate relative to that found in eastern populations. However, residents in Wyoming perceived that the density of white-tailed jackrabbits was much lower in 1985-87 than during years with peak populations, 1980-81.

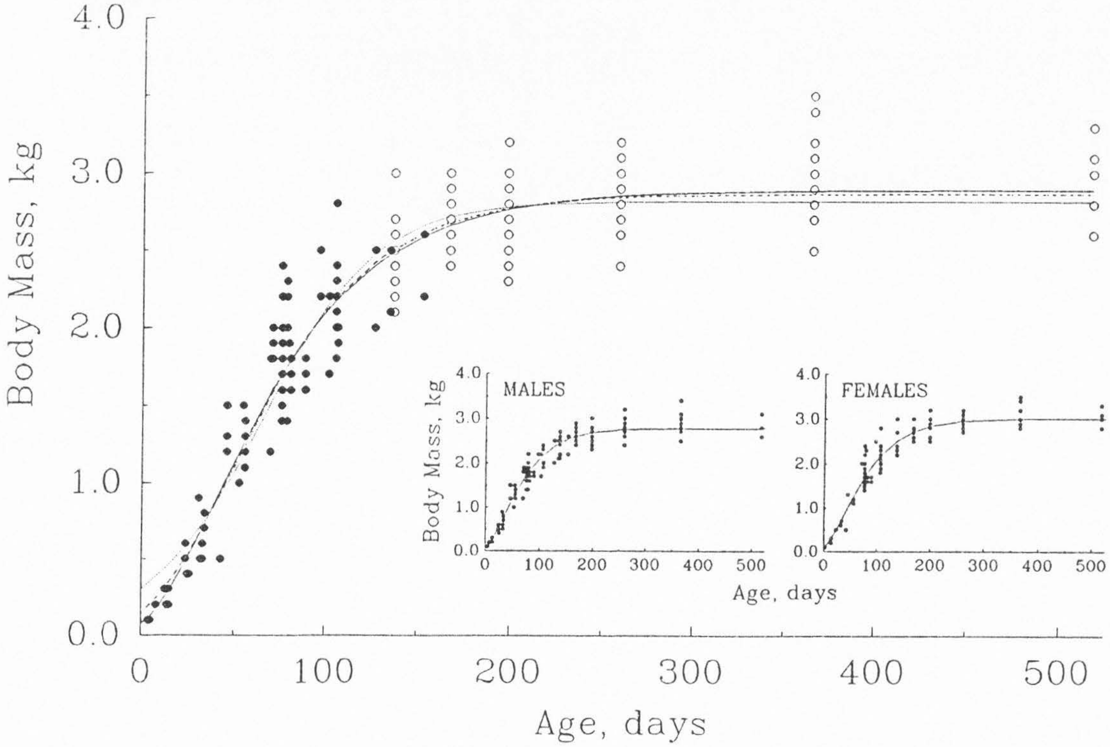

Fig. 8. Sigmoidal growth pattern of non-reproductive white-tailed jackrabbits based on body masses of captive (solid circles) and wild animals (open circles). The fit of Bertalanffy (dashed line), Gompertz (dotted line), and logistic (solid line) curves to all data are shown. The inset shows the fit of Bertalanffy curves to male and female data.

Table 3. Estimates of parameters of sigmoid curves fit to age-specific body masses (kg) of white-tailed jackrabbits: asymptotic body mass (A), growth rate constant (G), and inflection point (I). The predicted birth mass (B; kg), coefficient of determination ($\underline{R}^2_a$) and sample size ($\underline{n}$) are given.

Equation	A	G	I	B	$\underline{R}^2_a$	$\underline{n}$
Von Bertalanffy						
Males	2.78	0.021	35.98	0.068	0.926	137
Females	3.02	0.018	40.46	0.089	0.919	111
All	2.89	0.019	39.05	0.078	0.927	254
Gompertz						
Males	2.76	0.024	44.48	0.151	0.924	137
Females	2.99	0.021	49.57	0.176	0.917	111
All	2.87	0.023	48.00	0.140	0.925	254
Logistic						
Males	2.72	0.034	61.16	0.302	0.915	137
Females	2.95	0.028	67.78	0.385	0.905	111
All	2.82	0.032	65.39	0.310	0.917	254

An equal sex ratio appears to be common in jackrabbit populations. A 1:1 sex ratio is indicated for white-tailed jackrabbits collected in Iowa (Kline 1963). The sex ratio of white-tailed jackrabbits collected in Wyoming also did not differ significantly from parity. A sex ratio similar to 1:1 is also found in collections of black-tailed jackrabbits (L. californicus) (Lechleitener 1959, Tiemeier 1965, Gross et al. 1974, and others).

Collections of adult jackrabbits indicated that older animals were the least abundant in Wyoming. Fewer than 1% of collected jackrabbits were greater than 2 years-old, which implies either that the life span was less than 2 years or that older animals evaded collection. Since the sample size was large, 358 jackrabbits, and few sighted jackrabbits were not collected, I surmise that the life span of wild jackrabbits is seldom greater than 2 years. This agrees with the estimated life span for black-tailed jackrabbits, 1.8 years (Tiemeier 1965).

Sexual dimorphism in body mass is significant in white-tailed jackrabbits in Iowa (Kline 1963), Colorado (Bear and Hansen 1966), and North Dakota (James and Seabloom 1969b). I found a similar pattern of dimorphism in white-tailed jackrabbits in Wyoming. Sexual dimorphism apparently develops with maturation because a difference in body mass between sexes occurred only in jackrabbits that were >150 days-old. Greater body size in adult females may facilitate their production of large, precocial young (Millar 1981). Ralls (1976) suggests ultimate factors that could increase female body size.

Body masses of white-tailed jackrabbits varied among individuals of a given age (Figs. 7 and 8). Differences in body mass depend partly on gut mass, which varies with feeding activity of individuals (Robbins 1983). Some of the variation in body masses of young animals is caused by differences in individual growth rate: The range in growth rate of 25-100 day-old captive jackrabbits was 18 to 27 g/day even though food was available ad lib.

The average growth rate of white-tailed jackrabbits in Wyoming was 20 g/day from birth to two-thirds asymptotic body mass (2.9 kg), based on data of captive and field animals. This growth rate agrees with that of Lepus species of similar body mass (reviewed by Anderson and Lent 1977, Flux 1981). The average growth rate of hand-reared white-tailed jackrabbits in Colorado, 23 g/day (Bear and Hansen 1966), was slightly higher, perhaps because of better nutrition.

Zullinger et al. (1984) showed that the von Bertalanffy curve describes more variance in age-specific body masses of mammals than the Gompertz or logistic curves when data for early and asymptotic phases of growth are available. They reported that the Gompertz and logistic curves overestimate birth mass, whereas the von Bertalanffy curve slightly underestimates birth mass. A similar trend occurred when the three growth curves were fit to jackrabbit data. However, each curve described a similar amount of variance in jackrabbit body mass. Because the von Bertalanffy curve provided the best fit to birth mass, it was used to simulate postnatal growth (Chapter IX).

CHAPTER V

ENVIRONMENTAL INFLUENCES ON JACKRABBIT ACTIVITY

Radio-telemetry showed that free-living white-tailed jackrabbits became active within 1 hr after sunset and ceased activity by sunrise throughout the year. The onset was later relative to sunset and the cessation was earlier relative to sunrise during winter than during other seasons. The duration of the activity phase, from activity onset to cessation, was correlated with photoperiod (r = -0.998). Visual observations showed that jackrabbits were the most active from February to April, the beginning of the breeding season. Least movement and the greatest duration of foraging occurred when snow cover was present. Slightly lower activity occurred with precipitation or lower air temperature within a season. Jackrabbit movement rate increased with coyote howling and the movement distance, duration, and frequency decreased with moonlight.

INTRODUCTION

Environmental variables appear to constrain the timing and extent of seasonal activity in *Lepus* species. Changes in photoperiod are correlated with the duration of the daytime resting period in snowshoe hares (*Lepus americanus*) (Mech et al. 1966). A daytime resting phase followed by an activity phase coincident with declining light is apparent in many *Lepus* species (Tiemeier 1965, Knowlton et al. 1968, Bayfield and Hewson 1975, Costa et al. 1976, Lemnell and Lindlöf 1981, Matuszewski 1981). Weather conditions such as snowfall, wind, low air temperature, and precipitation may inhibit activity (Lechleitener 1958, Bider 1961, Tiemeier 1965, Lindlöf 1978). Snow cover could reduce movement (Severaid 1942, Bider 1961, Bear and Hansen 1966, Meslow and Keith 1971, Lindlöf et al. 1974, Stoddart 1985). In addition to effects of these physical variables, behavioral interactions including those with predators are important influences on activity pattern (reviewed by Cowan and Bell 1986).

Visual observations suggest that the activity of white-tailed jackrabbits (L. townsendii) is primarily nocturnal (Kline 1963, Bear and Hansen 1966), although some daytime activity may occur during mating (Kline 1963). Radio-telemetry of jackrabbits in Colorado indicates that their activity varies seasonally (Donoho 1972). Many other aspects of white-tailed jackrabbit activity have not been described in the literature. The objectives of this study were to (1) describe the diurnal activity rhythm of white-tailed jackrabbit and (2) examine the effects of season, weather, lunar phase, and predator activity on their movement patterns during the night.

METHODS

Radiotelemetry

Thirty-one white-tailed jackrabbits were live-trapped and fitted with 148-150 MHz radio-collars at a field site 10 km NW of Carter, Uinta County, Wyoming, during 1986-87 (Fig. 1). Radio signals were detected using a Telonics receiver connected to a mast-mounted, 5-element yagi antenna and monitored within a 2-km range from a tracking shelter on a hill. The radio-transmitters (Telemetry Systems) contained a mercury a mercury tip-switch and emitted a constant or erratic signal depending on whether animals were stationary or moving, respectively. Such transmitters provide reliable information on the magnitude and type of activity (Garshelis et al. 1982). Locomotion was readily differentiated from postural adjustment by changes in signal quality, verified by observing telemetered animals.

Because movements of radio-collared jackrabbits were detected very rarely during daylight, their radio transmissions were monitored regularly only 2 hr before and after sunset and sunrise. Signals from radio-collared individuals were monitored sequentially at 1.5 min intervals, during which a determination was made whether an animal was resting or ambulatory. The activity onset and cessation times detected by this means were compared with sunset and sunrise times at Sheridan, Wyoming (U.S. Nautical Alamanac Office 1977).

Direct Observations

The nighttime activity of jackrabbits was observed in a 0.5 ha, fenced compound at the USDA (APHIS) predator research station, Millville, Cache County, Utah. A polar coordinate grid was delineated in the compound with metal stakes and jackrabbits were observed from a tower (Fig. 9). The observer's eye level was approximately 7 m above ground level. Jackrabbits often moved too rapidly to be detected with a night vision scope. Therefore, the compound was illuminated dimly with lamps (Sylvania Capsylite, 150 W) mounted on the tower (two lamps) and poles at gridpoints A4 and I4 (one lamp per pole). Tiemeier (1965) and Drake (1969) concluded that artificial lighting has no visible effect on jackrabbit behavior. Jackrabbits were released into the compound at least 5 days before observations began to familiarize them with the area. It appeared that their movement was not inhibited by lighting because the animals were active throughout the compound.

Observations of white-tailed jackrabbits in the compound were conducted during three, 3-hr periods. The first began 1 hr after sunset, the second encompassed the night midpoint, and the third ended 1 hr before sunrise. The observer arrived 1 hr before the 3-hr period to minimize possible disturbance. During each observation hour, the number of movement bouts was counted and timed with a stopwatch and the path of the movements was traced on a scaled-down map of the enclosure (the movement distance was calculated later with a map measurer). The occurrence of coyote howling was noted. Coyotes were housed in kennels 0.2 km from the compound. Also, the duration of feeding activity was timed during the last 7 months of observations. Ambient conditions were recorded at the start of each observation hour (described below). Preliminary observations of 3 solitary male jackrabbits were conducted during 55 hr from January to June, 1986. For the more complete movement analysis that follows, jackrabbit activity was observed during November, 1986, to June, 1987, with solitary animals (3 males, 27 hr; 3 females, 27 hr) and groups of 2 animals of the same sex (2 males, 18 hr; 2 females, 17 hr) or the opposite sex (male with female: 2 males, 18 hr; female with male: 2 females, 15 hr).

The dependent variables used in the activity analysis were DIST = distance moved (m), TIME = duration of movement (s), MOVES = number of moves, and RATE = rate of movement during activity bouts (m/s), where the measurement period was 1 hr for each variable. The independent

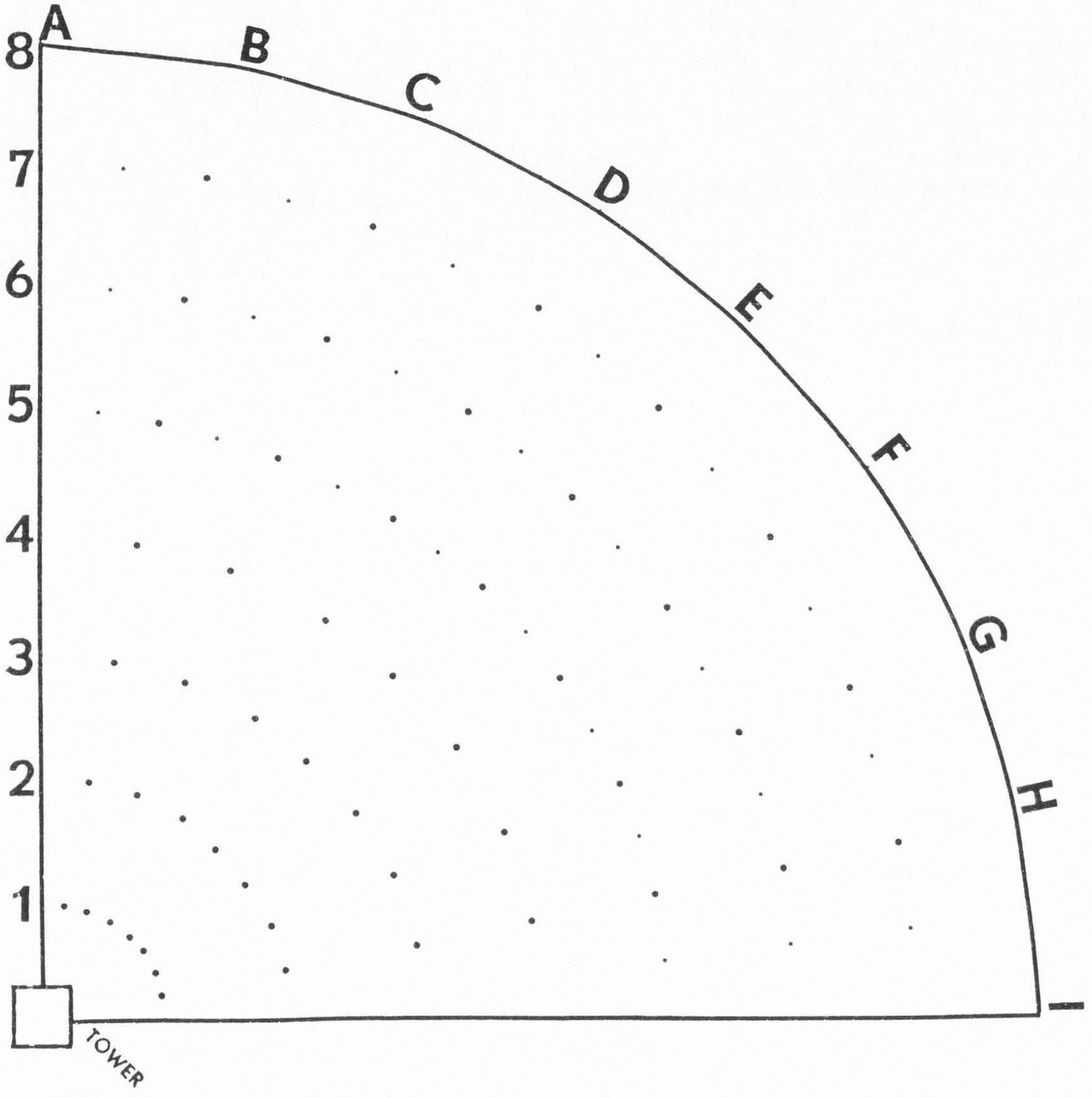

Fig. 9. Diagram of 0.5 ha compound used for visual observations of jackrabbits showing the observation tower and polar coordinate grid.

variables included COYOTE (0 = coyotes did not howl during the observation hour, 1 = coyotes howled), LUNAR (0 = day of observation was in the dark half of the lunar cycle, 1 = day was in the bright half of the cycle), SEASON (0 = early summer [May-June], 1 = autumn to winter [November-December], 2 = winter [January-February], 3 = spring [March-April]), BLOCK (0 = following dusk, 1 = surrounding the night midpoint, 2 = before dawn; as above), CLOUD cover (0 = <25%, 1 = 25 to 49%, 2 = 50 to 74%, 3 = $\geq$75%), SNOW cover (0 = snow on ground, 1 = no snow); air TEMPERATURE (0 = -19 to -10 °C, 1 = -9 to 0 °C, 2 = 1 to 10 °C, 2 = 11 to 20 °C), and PRECIPITATION (0 = none, 1 = rain, 2 = snow). Other independent variables were manipulated: ALONE (0 = animal alone in compound, 1 = two animals in compound) and SEX (0 = male, 1 = female).

RESULTS

Activity of Free-Living Jackrabbits

Sixteen of the 31 radio-collared jackrabbits were known to remain on the area. Nine of these were recaptured and six died. Fates of the other animals could not be determined.

Radio-telemetry indicated that the nocturnal activity of white-tailed jackrabbits usually commenced within 1 hr after sunset and ceased shortly before or at sunrise (Fig. 10). In comparison to other seasons, the winter activity began slightly later relative to sunset and ended earlier relative to sunrise. Individual jackrabbits often became active at about the same time. The duration of the activity phase between the activity onset and cessation (Y) was a function of the photoperiod (X): $Y = 20.89 - 0.814 \cdot X$, $\underline{r} = -0.998$, with X and Y expressed in hours.

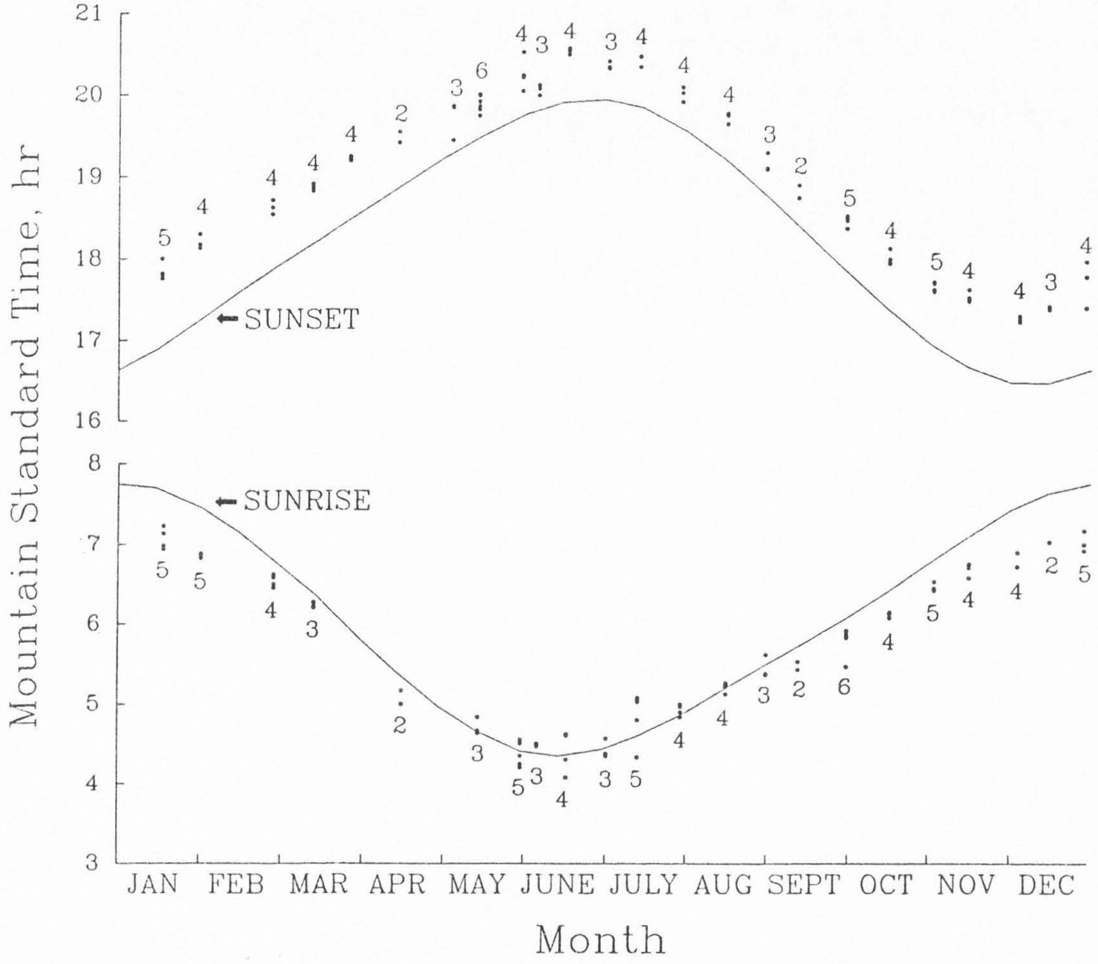

Fig. 10. The onset and cessation of activity of radio-collared jackrabbits in relation to sunrise and sunset times. Sample sizes are reported. Observations of individual jackrabbits (indicated as dots) may overlap.

When jackrabbits were telemetered during the daytime, no activity or only slight shifts in position were detected unless animals were disturbed by approaching them too closely. The nighttime activity was variable, with extended rest periods during which no locomotion was detected.

High winds were observed in Wyoming when estimating the activity onset on 17 June 1986, 15 November 1986, and 29 December 1986 and cessation on 18 January 1987. The activity onset and cessation on a windy day deviated only once from the yearly trend (Fig. 10). Two animals began activity later than expected on 29 December 1986.

Nighttime Movement Pattern

The movements of white-tailed jackrabbits, observed in the compound during the nighttime activity phase, were assumed to be representative of those of wild animals for several reasons: The vegetation structure in the compound, low shrub and bunchgrasses, was similar to that occurring in natural habitats. Predator influences were not prevented. Great horned owls (Bubo virginianus) pursued jackrabbits in the compound. Red fox (Vulpes fulva) attempted to attack jackrabbits from the outside of the fenced compound. The activity of jackrabbits in the compound and that of free-living jackrabbits telemetered in Wyoming were compared during June, 1987. The number of movement bouts/hr was similar in the compound (12 ± 3 [n = 18 hr; mean ± SE]) and in Wyoming (14 ± 1.5 [n = 34 hr]). Also, the duration of activity/hr was similar in the compound (92 ± 37 s [n = 18 hr]) and in Wyoming (107 ± 25 s [n = 24 hr]).

The nighttime movement patterns of white-tailed jackrabbits were analyzed with multivariate techniques described by Afifi and Clark (1984). Factor analysis was employed to estimate (over all observation hours) the degree of association between environmental variables that were measured (Table 4). Seasonal and weather variables were prominent in factors 1 and 2 and explained about 50% of the variance in the independent variables. CLOUD, PRECIPITATION, and SNOW were correlated in factor 1. SEASON, TEMPERATURE, and SNOW were correlated in factor 2. A relationship between COYOTE and BLOCK, namely more howling of coyotes in the early night, was indicated chiefly by factor 3. The remaining variance in the independent variables was due to changes in the lunar cycle, LUNAR, in factor 4.

The dependent variables DIST, TIME, and MOVES were interrelated. The correlation coefficients of DIST with TIME, DIST with MOVES, and TIME with MOVES were 0.98, 0.90, and 0.92, respectively. However, RATE had no clear correlation with DIST ($\underline{r} = 0.17$), TIME ($\underline{r} = 0.09$), or MOVES ($\underline{r} = 0.15$). Over all data, the dependent variables were highly variable, DIST = 719 ± 78.9, TIME = 339 ± 36.0, MOVES = 38 ± 3.2, and RATE = 2.0 ± 0.07.

A series of univariate ANOVAs were conducted to detect the more prominent effects of the independent variables on the activity variables (Table 5). A lower probability ($\underline{P}$) in the $\underline{F}$ test suggested but did not necessarily indicate a major effect because of the intercorrelation among the independent variables. Low probability values ($\underline{P} < 0.001$) were found in $\underline{F}$ tests of each dependent variable with SEASON. $\underline{F}$ tests

Table 4. Factor analysis of environmental variables. Factor loadings, eigenvalues, and percent variance explained by a factor are shown (after one varimax rotation). Positively correlated variables have a loading of similar sign within a factor.

Independent Variable	Factor 1	Factor 2	Factor 3	Factor 4
Coyote	0.06	0.18	0.84	0.02
Lunar	-0.14	0.02	-0.03	-0.96
Season	0.10	0.86	0.07	0.27
Block	-0.13	0.19	-0.76	-0.02
Cloud	-0.90	-0.08	-0.15	0.01
Snow	-0.52	0.47	0.28	-0.26
Temperature	0.05	-0.85	0.14	0.28
Precipitation	-0.86	0.01	-0.15	-0.16
Eigenvalue	2.2	1.8	1.3	0.9
Variance	28.2	22.0	15.9	11.8

Table 5. Univariate analyses of jackrabbit activity. Probability values (P) for F tests are approximate (see text).

DEPENDENT/ Independent Variable	Factor Level												
	0			1			2			3			
	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	$\bar{x}$	SE	n	P
MOVES (number)													
Coyote	39	4	69	38	5	54							0.794
Lunar	47	4	63	30	4	60							0.006
Season	10	5	27	29	4	36	33	5	27	76	4	33	<0.001
Block	36	5	42	34	6	39	44	5	42				0.462
Cloud	38	4	84	60	9	15	27	12	8	25	8	16	0.026
Snow	41	4	93	30	6	30							0.151
Temperature	2	18	3	50	5	47	41	4	52	11	7	21	<0.001
Precipitation	41	3	106	6	17	4	27	10	13				0.065
Alone	40	5	54	37	4	69							0.709
Sex	37	4	63	39	4	60							0.716
RATE (m/s)													
Coyote	1.8	0.1	69	2.2	0.1	54							<0.001
Lunar	2.0	0.9	63	1.9	0.1	60							0.363
Season	1.5	0.1	27	2.0	0.1	36	2.5	0.1	27	2.0	0.1	33	<0.001
Block	2.2	0.1	42	1.9	0.1	39	1.9	0.1	42				0.048
Cloud	2.0	0.1	84	2.0	0.2	15	2.6	0.2	8	1.6	0.2	16	0.027
Snow	1.9	0.1	93	2.4	0.1	30							<0.001
Temperature	2.2	0.4	3	2.1	0.1	47	2.1	0.1	52	1.6	0.2	21	0.045
Precipitation	2.0	0.1	106	1.2	0.4	4	2.0	0.2	13				0.062
Alone	2.1	0.1	54	2.0	0.9	69							0.301
Sex	2.1	0.1	63	1.8	0.1	60							0.016

Table 5. Continued.

	Factor Level												
DEPENDENT/ Independent Variable	0			1			2			3			
	$\bar{X}$	SE	n	$\bar{X}$	SE	n	$\bar{X}$	SE	n	$\bar{X}$	SE	n	P
DIST (m)													
Coyote	718	106	69	720	120	54							0.991
Lunar	947	107	63	479	109	60							0.003
Season	126	114	27	347	99	36	533	114	27	1762	104	33	<0.001
Block	708	135	42	610	40	39	832	135	42				0.525
Cloud	768	94	84	1053	222	15	409	304	8	308	215	16	0.071
Snow	794	91	93	486	159	30							0.094
Temperature	174	79	3	964	121	47	772	115	52	142	181	21	0.014
Precipitation	788	84	106	57	432	4	357	240	13				0.074
Alone	880	118	54	593	104	69							0.070
Sex	810	110	63	623	113	60							0.238
TIME (s)													
Coyote	348	48	69	325	54	54							0.749
Lunar	435	49	63	236	50	60							0.005
Season	74	52	27	172	45	36	233	52	27	822	46	33	<0.001
Block	307	62	42	298	64	39	407	62	42				0.397
Cloud	354	43	84	513	101	15	189	139	8	169	98	16	0.071
Snow	379	41	93	213	72	30							0.048
Temperature	7	219	3	454	55	47	357	52	52	82	83	21	0.014
Precipitation	370	38	106	35	197	4	171	109	13				0.071
Alone	395	54	54	295	48	69							0.168
Sex	371	50	63	304	52	60							0.352

of DIST, TIME, or MOVES with LUNAR had $P < 0.006$. Several other tests such as of weather effects yielded lower probability values.

Probability values < 0.01 were found in F tests of RATE with SNOW or SEX. However, SNOW and SEX were confounded ($r = 0.55$) because more observations of females than males occurred when there was snow cover. SNOW explained the most variance in RATE, as shown by regressing RATE on both variables (SNOW: partial $r = 0.26$, $P = 0.004$; SEX: partial $r = -0.04$, $P = 0.638$). COYOTE and BLOCK were also correlated, $r = -0.36$, as indicated by factor 3, above. Although COYOTE and BLOCK each had $P < 0.01$ in F tests with RATE, COYOTE was the primary effect on RATE (COYOTE: partial $r = 0.25$, $P = 0.005$; BLOCK: partial $r = -0.10$, $P = 0.262$).

Subset and stepwise regression analyses were employed to identify five models that explained the most variance in the dependent variables. To minimize the possibility of Type II errors (i.e., failure to identify a model that is significant), the choice of each independent variable used initially was liberal, $P < 0.2$ in an F test (Table 5). Because of multicollinearity, an independent variable that had a low probability value in a single-factor F test was not necessarily significant when used in bivariate or multivariate regressions. That is, the variance attributed to one variable might actually be caused by a correlated variable. For the final, best fit multivariate regression models, the least correlated variables were selected, and each variable included was significant at $P < 0.05$.

The best fit models (Table 6) explained only 52%, 54%, and 48% of the variance in DIST, TIME, and MOVES, respectively. Examination of the

Table 6. Regression models that explained the most variance in activity. Degrees of freedom, probability values associated with F tests, and coefficients of multiple determination (R^2_a) are reported. Partial correlation coefficients are shown in order of model parameter listed.

DEPENDENT/ Independent Variables	df	P	R^2_a	Partial r
DIST				
Season, Snow	2	< 0.001	0.524	+0.722, -0.381
Season, Lunar	2	< 0.001	0.470	+0.662, -0.216
Season, Temperature	2	< 0.001	0.468	+0.668, +0.212
Season	1	< 0.001	0.448	+0.673
Lunar, Temperature	2	< 0.001	0.155	-0.345, -0.323
TIME				
Season, Snow	2	< 0.001	0.537	+0.728, -0.179
Season, Temperature	2	< 0.001	0.464	+0.664, +0.208
Season, Lunar	2	< 0.001	0.460	+0.658, -0.191
Season, Precipitation	2	< 0.001	0.458	+0.670, -0.179
Season	1	< 0.001	0.444	+0.670
MOVES				
Season, Snow	2	< 0.001	0.476	+0.690, -0.335
Season, Lunar	2	< 0.001	0.430	+0.635, -0.184
Season	1	< 0.001	0.415	+0.648
Lunar, Temperature	2	< 0.001	0.171	-0.337, -0.365
Temperature, Snow	2	< 0.001	0.126	-0.355, -0.256
RATE				
Snow, Season, Block	3	< 0.001	0.194	+0.315, +0.259, -0.239
Snow, Season, Coyote	3	< 0.001	0.187	+0.330, +0.228, +0.220
Snow, Season	2	< 0.001	0.153	+0.292, +0.254
Snow, Coyote	2	< 0.001	0.149	+0.282, +0.247
Snow, Block	2	< 0.001	0.144	+0.351, -0.235

partial correlation coefficients showed that SEASON explained the most variance in DIST, TIME, and MOVES (Table 6). The seasonal effect was caused by greater activity from February to April and reduced activity in early summer (Table 7).

Three weaker trends were found for DIST, TIME, and MOVES (Tables 5 and 6): (1) a decrease during the brightest portion of the lunar cycle, (2) an increase when air temperatures warmed within a season, i.e., partial *r* was positive after SEASON was adjusted for, and (3) a decrease with precipitation.

The best fit model for RATE explained only 19% of the variance, indicating the invariability of the movement rate. The independent variables had a small influence on RATE (Tables 5 and 6): (1) an increase with snow cover, (2) a similar trend with season as found for DIST, TIME, and MOVES, and (3) an increase when coyotes howled in the early night.

Wind speed effects were not included in the multivariate analyses because only 9 hr with high winds were noted. The magnitude of each dependent variable during windy hours did not vary significantly from mean hourly values (z tests, $P > 0.05$).

The duration of foraging by jackrabbits was estimated from January to June, 1987 (Table 7). Feeding and digging could not be separated during the winter because feeding is accomplished by digging in the snow. The foraging time estimate includes digging in addition to feeding during winter. The duration of foraging/hr was higher ($P < 0.001$) with snow cover (30 ± 3.7 min, $n = 21$) than with no snow (15 ± 1.8 min, $n = 60$).

Table 7. Monthly activity patterns of white-tailed jackrabbits (mean ± SE; sample size in parenthesis). Probability values associated with single-factor *F* tests are reported.

Dependent Variable	Month NOV	DEC	JAN	FEB	MAR	APR	MAY	JUNE	*P*
DIST (m)									
1986-87	372 ± 80 (21)	312 ± 59 (15)	344 ± 149 (9)	628 ± 143 (18)	1615 ± 161 (18)	1939 ± 310 (15)	58 ± 15 (9)	161 ± 65 (18)	< 0.001
1986	---	---	116 ± 48 (30)	361 ± 72 (13)	1946 ± 184 (2)	1218 ± 106 (6)	---	850 ± 130 (4)	< 0.001
TIME (s)									
1986-87	190 ± 42 (21)	148 ± 25 (15)	145 ± 64 (9)	278 ± 68 (18)	772 ± 71 (18)	883 ± 133 (15)	37 ± 10 (9)	92 ± 37 (18)	< 0.001
MOVES (number)									
1986-87	29 ± 2 (21)	30 ± 4 (15)	20 ± 8 (9)	39 ± 7 (18)	86 ± 7 (18)	64 ± 9 (15)	7 ± 2 (9)	12 ± 3 (18)	
RATE (m/s)									
1986-87	2.0 ± 0.2 (21)	1.9 ± 0.2 (15)	2.2 ± 0.3 (9)	2.6 ± 0.2 (18)	2.0 ± 0.1 (18)	2.1 ± 0.1 (15)	1.6 ± 0.3 (9)	1.5 ± 0.1 (18)	< 0.001
FORAGING (min)									
1987	---	---	25.3 ± 7.8 (6)	30.3 ± 3.6 (18)	14.6 ± 2.3 (18)	12.7 ± 2.6 (15)	11.5 ± 4.5 (9)	20.2 ± 4.6 (18)	< 0.005

DISCUSSION

White-tailed jackrabbits in Wyoming had a diurnal activity rhythm, with their nightly activity beginning shortly after dusk and ending by dawn. A circadian rhythm was also apparent because the duration of the activity phase was correlated with the photoperiod throughout the year, $\underline{r} = -0.998$. The strong correlation with photoperiod suggests that their activity pattern is tightly entrained to the seasonal cycle and suggests that there has been strong selection pressure for jackrabbits to be nocturnal, perhaps due to chronically high predation levels (Cowan and Bell 1986).

Selection for nocturnal activity appears to be prevalent in Lepus species. Radio-telemetry of snowshoe hares (L. americanus) in Minnesota from January to April shows that their movement begins close to or following sunset and ends before dawn (Mech et al. 1966). Black-tailed jackrabbits (L. californicus) in Arizona become active within 30 min of sunset and retreat to their daytime forms between dawn and sunrise each season (Costa et al. 1976). Black-tailed jackrabbits in other western states move between feeding and resting areas at dawn and dusk (Lechleitener 1958, Tiemeier 1965, Knowlton et al. 1968, Haug 1969). European hares (L. europeaus) and mountain hares (L. timidus) also increase activity during the crepuscular periods (Bayfield and Hewson 1975, Lemnell and Lindlöf 1981, Matuszewski 1981).

The activity of white-tailed jackrabbits began later relative to sunset and ended earlier relative to sunrise during the winter than during other seasons. Similarly, Mech et al. (1966) reported that the activity of snowshoe hares ceases earlier relative to sunrise during winter than during spring. They have posited that a certain threshold light intensity inhibits daytime activity. However, the duration of astronomical twilight increases from December to July (U.S. Naval Observatory 1946). Therefore, if a threshold light intensity inhibits activity, the winter onset and cessation should be the closest to sunset and sunrise, respectively, which is not the case.

The later onset and earlier cessation of winter activity, relative to sunset and sunrise times, may occur only because the nights are longest during the winter. The duration of the winter activity phase of the white-tailed jackrabbit appeared to be sufficiently lengthy to obtain sufficient food, 14 hr in December, without requiring a longer activity period. Jackrabbits may not need to feed actively during the entire period. The foraging time of animals in the compound was on average 30 min/hr when snow cover was present.

The presence of snow cover could depress nighttime activity. Reduced activity following snowfall occurs in snowshoe hares (Severaid 1942, Meslow and Keith 1971) and mountain hares (Lindlöf et al. 1974). Jackrabbits may have difficulty running in deep snow (Bear and Hansen 1966, Stoddart 1985). At the Millville compound, white-tailed jackrabbits moved 27% less often and 39% shorter distances when snow cover was present. Also, the foraging time was twice as great with snow cover as without snow cover. Reduced movement would lower locomotory energy expenditure (Tayor and Heglund 1982), whereas increased foraging could maximize energy intake during winter.

An increase activity during the late winter (the onset of the breeding season) occurs in many Lepus spp. Black-tailed jackrabbits in

Arizona are more active in March than in summer or winter (Costa et al. 1976). White-tailed and black-tailed jackrabbits in Colorado increase activity from March to April (Donoho 1972). The aggressive behavior of European hares in Sweden increases during mid-March (Lindlöf 1978). Mountain hares in Sweden are more active in late winter than in early winter (Lindlöf et al. 1974). In the present study, the activity of white-tailed jackrabbits increased during February, peaked in March and April, and declined subsequently (Table 7). Chasing and leaping, which are associated with breeding in jackrabbits (Lechleitener 1958, Blackburn 1968), increased during the late-winter. Most of the variance in jackrabbit activity was explained by greater late-winter movement, relative to that in other seasons, indicating the importance of the late-winter behaviors for the species.

The pattern of activity during the night appears to vary between individuals of a species and between Lepus species. Snowshoe hare activity increases during the night, peaks at 2300 hr, and declines (Keith 1964). In contrast, combined data for white-tailed and black-tailed jackrabbits indicates no clear hourly trend in nighttime movements and considerable variance each hour (Donoho 1972). In the present study, the movement distance, duration, and frequency also varied among individual white-tailed jackrabbits, with no significant hourly trend. The coefficient of variation (SE·100/mean) was 11% for the distance moved, 11% for the duration of movement, and 8% for the number of moves. Jackrabbits often rested during the night for a variable period. Over all observations, jackrabbits moved only 12 ± 1.3

min/hr. Substantial nocturnal resting has also been observed in black-tailed jackrabbits (Lechleitener 1958, Drake 1969, Costa et al. 1976).

Predator aversion has an important influence on activity in Lepus species (reviewed by Cowan and Bell 1986). In the present study, the average movement rate of white-tailed jackrabbits increased from 1.8 to 2.2 m/s (22%) when coyotes howled during the early-night, which could expedite their escape from this potential predator. The increase was significant because the coefficient of variation for the movement rate was relatively small, 4%. White-tailed jackrabbits also moved 49% less far and 36% less frequently during the brightest half of the lunar cycle, which may be a tactic to avoid detection by predators. Activity inhibition in moonlight occurs in several small mammals (Lockard and Owings 1974, Morrison 1978, Wolton 1983).

Weather variables explained little of the variance in the activity of the white-tailed jackrabbit. Although precipitation and lower temperatures within a season reduced activity slightly (Table 6), high winds did not appear to affect movements or the onset and cessation of nighttime activity. Previous observations suggest that there is considerable variance in individual response to weather. In black-tailed jackrabbits, precipitation or wind may reduce activity (Lechleitener 1958) or have no apparent effect (Costa et al. 1976). Haug (1969) found no correlation of air temperature, wind speed, or precipitation with the activity pattern of black-tailed jackrabbits. The activity of mountain hares may decrease during snowfall (Lindlöf 1978) but two animals of this species moved 11.3 km during blizzard conditions (Flux 1970).

Weather effects might only be marked under extreme conditions. Snowshoe hares are less active following fresh snowfall when air temperatures are bitter cold (Severaid 1942, Bider 1961, Meslow and Keith 1971). Black-tailed jackrabbits may seek shelter during extremely cold, windy, winter storms (Tiemeier 1965, Stoddart 1985).

CHAPTER VI

SEASONAL, ENERGETIC ADAPTATIONS OF THE JACKRABBIT

Variations in energy use and thermal conductance are described for white-tailed jackrabbits (Lepus townsendii) acclimatized to winter or summer conditions. The basal metabolic rate (BMR) was higher ($P < 0.0001$) in winter- than in summer-acclimatized jackrabbits and the winter BMR was higher ($P < 0.0001$) than that predicted by Kleiber (1961). During winter, jackrabbits had a thicker pelage ($P < 0.001$) and a lower overall thermal conductance (C) ($P < 0.001$) than during summer. The body temperature was also higher ($P < 0.001$) in winter- than in summer-acclimatized jackrabbits, and the ratio BMR:C was greatest in winter. Variations in BMR and C contributed to a 17 °C decline in the lower critical temperature (LCT) from summer to winter. The decline in LCT and thermal conductance lowered the energy use of winter (versus summer) animals at colder air temperatures, whereas lower BMR lowered the energy use of summer (versus winter) animals at warmer temperatures. Estimated thermoregulatory cost due to air temperatures below LCT was slight in white-tailed jackrabbits acclimatized to conditions in either season.

INTRODUCTION

Temperate zone mammals are exposed to seasonal variations in ambient temperature and exhibit physiological changes that ultimately can reduce their heat loss and energy expenditure in cold environments. Various strategies are employed for cold adaptation in endotherms

(Chaffee and Roberts 1971, Hart 1973, Webster 1974). Leporids (rabbits and hares) show a significant seasonal variation in insulation and heat transfer through the fur (Scholander et al. 1950, Hart 1956, Hart et al. 1965, Harris et al. 1985). In three leporid species, desert cottontails (Sylvilagus audubonii), black-tailed jackrabbits (Lepus californicus), and antelope jackrabbits (L. alleni), the thermal conductance is lower but the basal metabolic rate (BMR) is higher in winter than in summer (Hinds 1973, 1977). Seasonal variation in shivering (Hart et al. 1965) and non-shivering thermogenesis (Feist and Rosenmann 1975) occurs in snowshoe hares (L. americanus). Complex interactions, which determine the direction of heat flow between an animal and its environment (Gates 1980), can influence the total energy expenditure each season (Shoemaker et al. 1976).

The seasonal, physiological variation of white-tailed jackrabbits (L. townsendii) has not been described previously. Thus, the aims of this study were to test for physiological variation in the jackrabbit and compare seasonal adaptations of jackrabbits with those previously demonstrated in other leporids. Because the species is widely distributed in North American prairie ecosystems (Hall 1981), but occupies a different ecological niche than other leporids (Dunn et al. 1982), its physiological adaptations could differ from those of other leporids.

METHODS

White-tailed jackrabbits were trapped 12 km south of Granger, Sweetwater County, Wyoming, and transported to Green Canyon Ecology Compound, Utah State University, Logan, UT. They were maintained in large, outdoor pens for 4-6 months before experiments began, and supplied with commercial rabbit food, apples, and free water. Physiological experiments with three jackrabbits of each sex were conducted during daylight hours (the resting phase of jackrabbits) in July-August, 1986, and January-February, 1987. The animals weighed 2.43 ± 0.04 kg (mean ± SE) in summer and 2.81 ± 0.04 in winter experiments.

The oxygen consumption of winter- and summer-acclimatized jackrabbits was determined using an open-flow, indirect calorimetry system. Air was pumped (10 l/min) from an 86 l metabolism chamber in which an animal was placed. Oxygen content was analyzed in a stream of moisture- and CO_2-free air (S-3A, Applied Electrochemistry) and the rate of oxygen consumption, $\dot{V}O_2$ (ml $O_2 \cdot (g \cdot hr)^{-1}$), was calculated at STP with Equation 2 in Hill (1972). Air temperatures (T_a) used in experiments were randomly selected from -5, 2, 9, 16, 23, and 30 °C in summer and -19, -12, -5, 2, 9, and 16 °C in winter. O_2 content was measured during 90 min at each air temperature, with at least 60 min to establish thermal equilibrium at a different temperature. $\dot{V}O_2$ was extremely stable because jackrabbits were usually docile once in the metabolism chamber. If activity occurred, a trial was prolonged until a stable record could be obtained for at least 40 min. Basal metabolic rate (BMR), the metabolic rate fasted animals at rest in thermoneutrality (Bligh and Johnson 1973), was estimated as mean $\dot{V}O_2$ during 40 min when $\dot{V}O_2$ was lowest. Lower critical temperature (LCT) was determined as the air temperature below which $\dot{V}O_2$ increased.

A body temperature transmitter (Minimitter; VM-disk) calibrated to ± 0.1 °C was implanted abdominally into each jackrabbit (sutured to the peritoneum at the linea alba). The emitted signal was detected with an antenna looped around the inner walls of the metabolism chamber and relayed to an AM receiver. The body temperature of a jackrabbit was determined by counting the transmitted pulse frequency during steady periods of oxygen consumption (thrice per animal per air temperature).

The metabolism chamber consisted of a metal container with an acrylic window above the animal. A jackrabbit was placed into the chamber on the evening prior to an experiment. This allowed 10-12 hr for an animal to attain post-absorptive condition. Air temperature in the chamber was monitored by thermocouple and regulated to ± 1 °C. To reduce conductive heat exchange during experiments, a wire mesh was placed 2 cm above the chamber floor. Inner walls were painted flat black to decrease reflection (Porter 1969). Each animal was held in the chamber on at least five occasions before commencement of the study.

To assess seasonal differences in heat exchange between live jackrabbits exposed to winter or summer conditions, overall thermal conductance (C) was estimated under standard laboratory conditions (i.e., calm air, reduced conduction and radiative flux). Overall thermal conductance was estimated below LCT using the Scholander-Irving model, $C = \dot{V}O_2/(T_b - T_a)$, described in Hart (1973) and McNab (1980).

Fur thickness (the distance from the skin to the tip of an extended guard hair) was measured in the dorsal-lumbar region of brown-phase jackrabbits in September and white-phase jackrabbits in March. Because insulation in mammals increases with the thickness of fur (Scholander et al. 1950, Hart 1956, McClure and Porter 1983), this provided a relative index of insulation.

Ambient temperature at 0.2 m above ground level (jackrabbit height) was recorded continuously in sagebrush-grassland habitat at Carter and 10 km NW of Carter, Uinta County, southwestern Wyoming. Thermographs were calibrated to ± 1 °C and placed in ventilated shelters. Temperatures were sampled at 2 hr intervals from the thermograph chart records. Because temperatures did not differ significantly ($\underline{P} > 0.05$) between locations, only Carter data are reported. A FORTRAN program was written to compute the means and variances of air temperatures recorded during the daytime and the nighttime (daily temperature records were partitioned by daylength).

ANOVAs or t-tests were used to estimate the probability of a difference in metabolic rate, thermal conductance, or body temperature between seasons or between animals within a season. Least square regressions were derived to examine seasonal trends in energy use.

RESULTS

Metabolic data for male and female jackrabbits were pooled each season because differences were not detected by sex ($\underline{P} > 0.05$). BMR was lower ($\underline{P} < 0.0001$) in summer-acclimatized (brown-phase) than in winter-acclimatized (white-phase) animals (Fig. 11). Summer BMR, 0.52 ± 0.013 ml $O_2 \cdot (g \cdot hr)^{-1}$ ($\underline{n} = 18$ [6 animals, 3 air temperatures]; mean ± SE), was similar ($\underline{P} = 0.12$) to the expected BMR from Kleiber's (1961) equation, 0.49 ml $O_2 \cdot (g \cdot hr)^{-1}$ but winter BMR, 0.63 ± 0.012 ($\underline{n} = 18$), was higher ($\underline{P} < 0.0001$) than expected BMR.

The lower critical temperature (LCT) declined from approximately 11 to -6 °C from summer to winter (Fig. 11). Equations to describe the rate of oxygen consumption ($\dot{V}O_2$) below the lower critical temperature were derived using the least squares method. Summer $\dot{V}O_2 = 0.711 - 0.0171 \cdot T_a$ ($\underline{r} = 0.93$, $\underline{n} = 18$ [6 animals, 3 air temperatures]). Winter $\dot{V}O_2 = 0.546 - 0.0147 \cdot T_a$ ($\underline{r} = 0.83$, $\underline{n} = 18$). Absolute values of slopes in $\dot{V}O_2$ equations (0.015 ml $O_2/g \cdot h \cdot °C$ in winter; 0.017 ml $O_2/g \cdot h \cdot °C$ in summer) were slightly biased estimators of overall thermal conductance because the X-axis intercepts for winter and summer, 41.6 and 37.1 °C, respectively, did not extrapolate to T_b at $\dot{V}O_2 = 0$ (Fig. 11). Therefore, overall thermal conductance was estimated by calculating the mean conductance of individual animals from concurrent measurements of $\dot{V}O_2$, T_b, and T_a at each air temperature below LCT, as recommended by McNab (1980). With this method, the overall thermal conductance remained lower, by 26%, in jackrabbits in winter, 0.014 ± 0.0003 ml $O_2/g \cdot h \cdot °C$, than in summer, 0.019 ± 0.0004 ml $O_2/g \cdot h \cdot °C$ ($\underline{P} < 0.001$).

The pelage was 14% thicker in white- than in brown-phase jackrabbits ($\underline{P} < 0.001$). Pelage depth was 32 ± 0.82 mm ($\underline{n} = 24$) in white-phase versus 28 ± 0.41 mm ($\underline{n} = 22$) in brown-phase animals.

The body temperatures (T_b) was higher ($\underline{P} < 0.001$) in winter-acclimatized, 38.9 ± 0.05 °C ($\underline{n} = 36$ [6 animals, 6 air temperatures]), than in summer-acclimatized jackrabbits, 38.2 ± 0.07 °C ($\underline{n} = 36$). Body temperatures were similar ($\underline{P} > 0.05$) within each season over a wide range of T_a (Fig. 11). Differences in body temperature were not detected between sexes ($\underline{P} > 0.05$).

Mean ambient temperatures in sagebrush-grassland habitat fell most frequently below LCT of brown-phase animals during May, September, and October and LCT of white-phase animals during early-winter (Fig. 12). During molt periods (April-May, October-November), mean temperatures

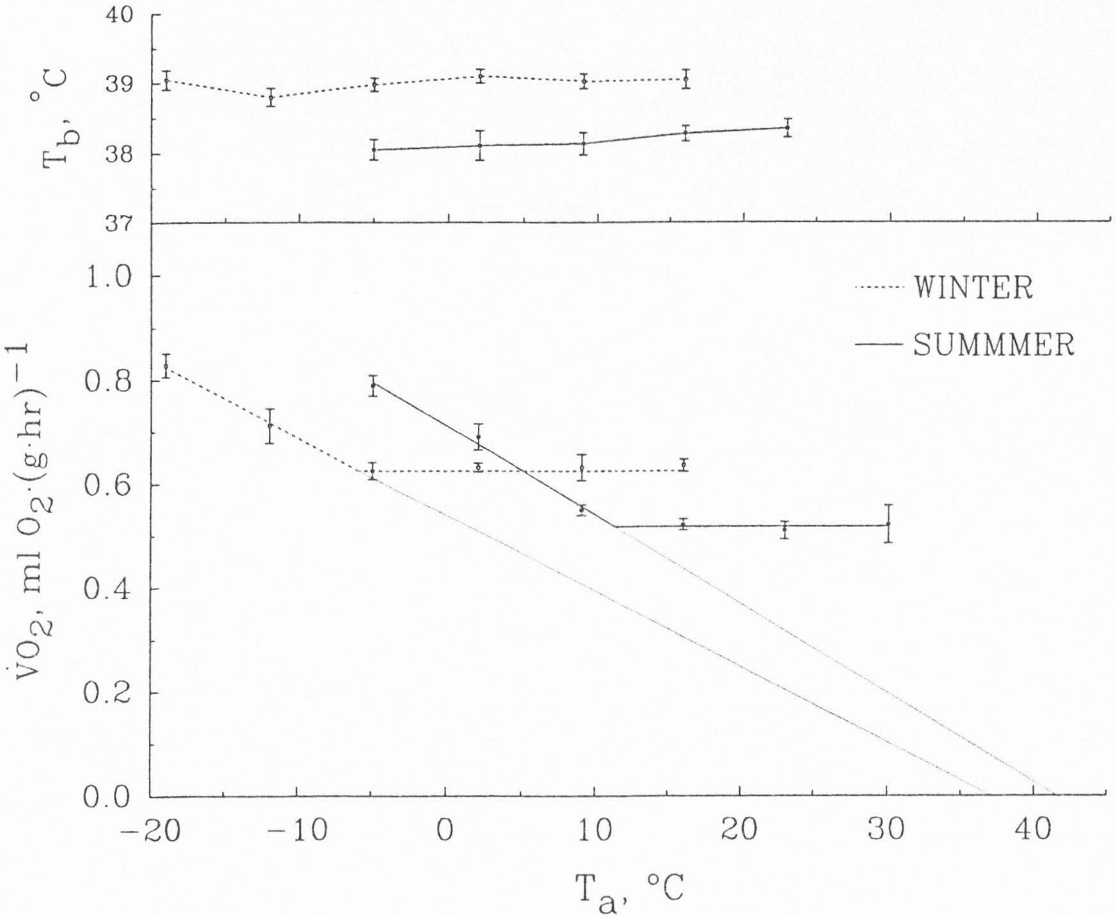

Fig 11. Rates of oxygen consumption ($\dot{V}O_2$) and body temperatures (T_b) of white-tailed jackrabbits acclimatized to conditions in winter (dashed line) or summer (solid line) (mean ± SE).

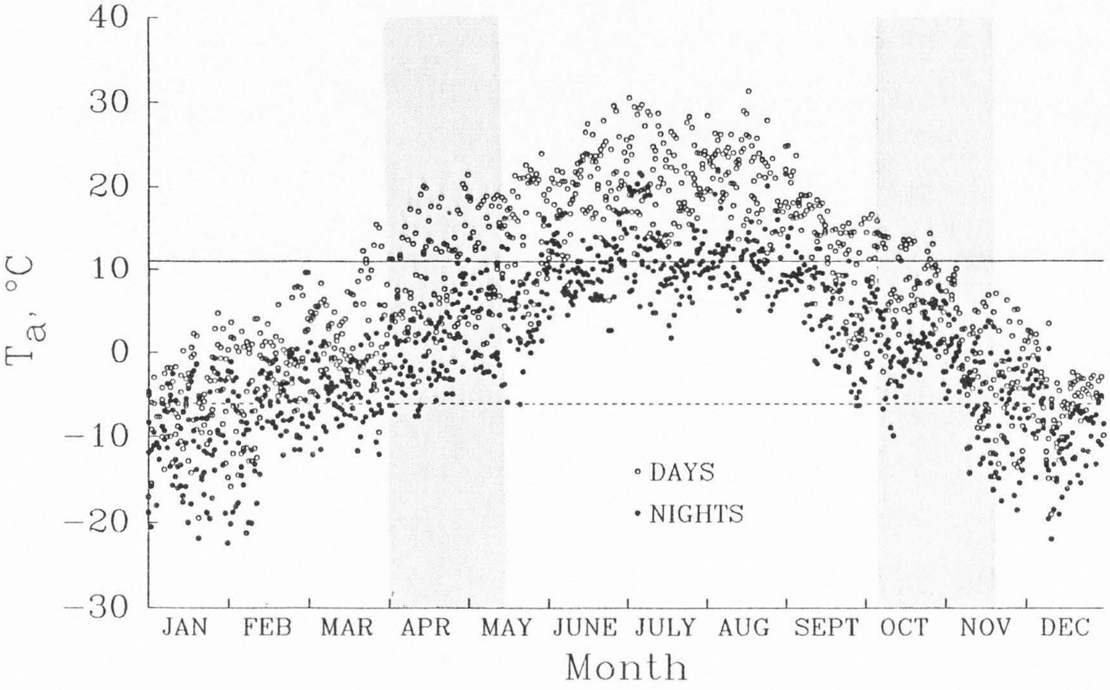

Fig. 12. Ambient temperatures (mean ± SE) at 0.2 m above ground level, Carter, Wyoming, in daytime (open circles) and nighttime hours (solid circles), 1985-87. Stippled areas indicate spring and autumn molt periods for white-tailed jackrabbits. Horizontal lines are the lower critical temperatures for brown-phase (solid line) and white-phase (dashed-line) animals.

were often between LCTs of white- and brown-phase animals. Mean daytime air temperatures were usually above LCT, but mean nighttime temperatures often fell below LCT.

DISCUSSION

The basal metabolic rate (BMR) varies seasonally in white-tailed jackrabbits. Winter BMR was 22% higher than summer BMR and 30% higher than BMR estimated by Kleiber's (1961) allometric equation. Because winter BMRs in desert cottontails, black-tailed jackrabbits, and antelope jackrabbits are also significantly higher than summer BMRs (Hinds 1973, 1977), ability to vary BMR seasonally appears to be a common adaptation among leporids. Hayssen and Lacy (1985) have presented an allometric curve that predicts mean BMR in leporids and other lagomorphs. With the addition of data for the white-tailed jackrabbit, it appears that two curves best describe BMRs of summer- and winter-acclimatized leporids (Fig. 13). Curves were derived using mean BMRs of North American leporids, from studies in which animals were considered to be post-absorptive. BMR for the arctic hare (_L. arcticus_) was not included in the curve for animals acclimatized to summer conditions because it had an atypically low BMR when measured in September (Wang et al. 1973).

Summer BMRs of North American leporids fell close to line described by Kleiber's (1961) equation, whereas winter BMRs were always above it (Fig. 13), which suggests that leporids elevate metabolism over standard level during winter. Metabolic increase could involve changes in thyroid hormone utilization (Andrews et al. 1978, Tomasi and Horwitz 1987) or catecholamine metabolism (reviewed by Chaffee and Roberts

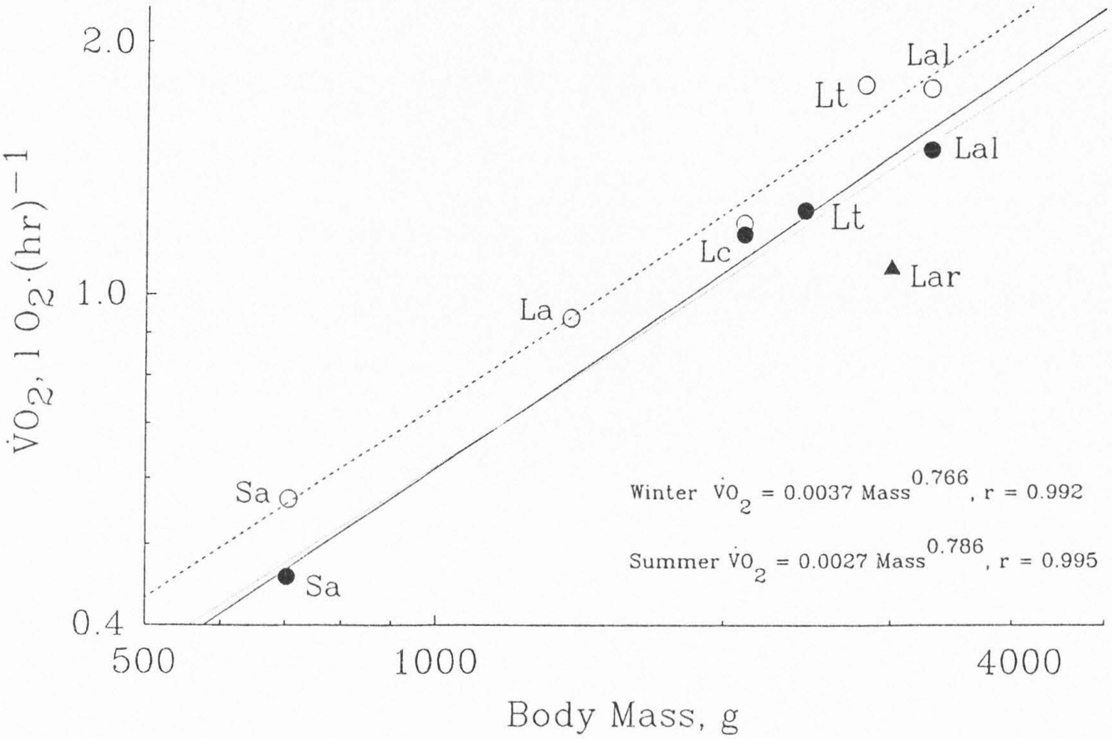

Fig 13. Basal rates of oxygen consumption in North American leporids. Data are means for summer- (solid circles) and winter-acclimatized animals (open circles). Least squares estimates of winter $\dot{V}O_2$ (dashed line) and summer $\dot{V}O_2$ (solid line) are shown. Dotted line indicates Kleiber's (1961) estimate of BMR (l O_2/hr = $0.0035 \cdot W_{(g)}^{0.75}$; 19.67 KJ/l O_2). Data are from Sylvilagus auduboni (Sa; Hinds 1973) , Lepus americanus (La; Irving et al. 1957), L. californicus (Lc; Hinds 1977), L. townsendii (Lt; this study), L. alleni (Lal; Hinds 1977), and L. arcticus (Lar; solid triangle; not included in summer equation [see text]; Wang et. al 1973).

1971, Webster 1974). Increased responsiveness to catecholamines has been demonstrated in cold-adapted rabbits (Oryctolagus cunniculus) (Heroux 1967, Kokova and Jansky 1968) and snowshoe hares (L. americanus) (Feist and Rosenmann 1975); these results may extrapolate to other leporids.

Overall thermal conductance was extremely low, 0.019 and 0.014 ml O_2/g·h·°C in white-tailed jackrabbits acclimatized to summer and winter conditions, respectively, and similar to that expected for equal-sized arctic mammals, 0.014 ml O_2/g·h·°C (equation in Robbins 1983:129). The thermal conductance expected for other (more average) mammals of equal weight is 0.026 ml O_2/g·h·°C (equation in Bradley and Deavers 1980). Low overall thermal conductance would reduce heat loss from the jackrabbit to the environment at colder ambient temperatures, and could adapt jackrabbits to more northerly, high elevation regions, where they occur (Dunn et al. 1982).

Seasonal variation of 20-35% has been demonstrated in thermal conductances of other North American leporids (Hart et al. 1965; Hinds 1973, 1977), except black-tailed jackrabbits, which have a greater seasonal, insulatory change (Hinds 1977). Overall thermal conductance in white-tailed jackrabbits declined by 26% from summer to winter, in general agreement with the pattern for leporids. The overall thermal conductance varied more between seasons than fur thickness (14%), which suggests that factors that may not be directly related to pelage thickness also contributed to the seasonal variation in thermal conductance.

Several avenues of sensible and insensible heat exchange can influence thermal conductance from the body core to the peripheral, boundary layer (Gates 1980). Changes in peripheral circulation have a major effect on heat flow in leporids (Honda et al. 1963, Gonzales et al. 1971, Kruk et al. 1981). Evaporative water loss dissipates metabolic heat production and varies seasonally (Hart et al. 1965; Dawson and Schmidt-Nielsen 1966; Hinds 1973, 1977). Convective, conductive, and radiative fluxes influence heat flow through the integument and pelage (reviewed by Harris et al. 1985).

McNab (1970) has shown that an increase in basal metabolic rate (BMR) relative to overall thermal conductance (C) can elevate body temperature because more heat is stored. Relative change in the ratio of BMR to C may account for the higher body temperatures I found in white-tailed jackrabbits during winter. The ratio was 45:1 in winter and 27:1 in summer jackrabbits. It is interesting that significant, seasonal variation in body temperature has not been demonstrated in other leporids (Hart et al. 1965; Hinds 1973, 1977) even though their BMR:C ratios increase by approximately as much between seasons. This suggests that overall heat flux could differ among leporids. However, BMR:C ratios and body temperatures higher than typical eutherians occur in all leporids previously studied (Wang et al. 1973) and in white-tailed jackrabbits.

Changes in BMR and C, and hence LCT, are adaptive in temperate-zone leporids because seasonal energy use can be lowered (Hart et al. 1965; Hinds 1973, 1977). In the white-tailed jackrabbits, higher BMR (by 21%) and lower C (by 26%) reduced the lower critical temperature by 17 °C from summer to winter (Fig. 1). Lower thermal conductance and LCT in winter-acclimatized, versus summer-acclimatized, jackrabbits reduced thermoregulatory energy use at colder ambient temperatures; lower BMR in summer-acclimatized, versus winter-acclimatized, jackrabbits reduced energy use at warmer T_a.

It appeared that seasonal acclimatization in jackrabbits coincided with the air temperature (5 °C) at which energy use would be minimized each season. Energy use was lower in white- than brown-phase white-tailed jackrabbits at $T_a < 5$ °C, and lower in brown-phase jackrabbits at $T_a > 5$ °C (Fig. 1). Mean air temperature varied around 5 °C during the molt periods, 1985-87 (Fig. 2). However, this inference is approximate if applied to free-living jackrabbits. Their energy use would depend on variables such as wind speed in the microhabitat, in addition to ambient temperature.

The rate of thermoregulatory energy use caused by air temperatures below LCT was relatively small in white-tailed jackrabbits acclimatized to summer or winter conditions, compared to mammals with a higher thermal conductance (Bradley and Deavers 1980). At air temperatures of 15 °C below LCT of brown- or white-phase animals, -4 and -21 °C, use of thermoregulatory energy (estimated from curves of $\dot{V}O_2$ on T_a) elevated the metabolic rates of fasted summer- and winter-acclimatized jackrabbits only to 1.50·BMR and 1.35·BMR, respectively.

Nighttime air temperatures in Wyoming fell below LCT of post-absorptive animals more often than daytime air temperatures and, therefore, could have induced thermoregulatory energy use more frequently. However, because specific dynamic activity (Kleiber 1961) and other heat fluxes, i.e., radiative (Hayes and Gessaman 1980), could decrease LCT, thermoregulatory energy use by wild jackrabbits may occur only at air temperatures substantially below fasted LCT.

CHAPTER VII

JUVENILE ENERGETICS AND DEVELOPMENT OF HOMEOTHERMY

Metabolic rate (MR) was highest in newborn white-tailed jackrabbits and declined with age. However, at 80-81 days-old, MR was still higher than that of adults. Rectal temperature (T_{re}) declined at low air temperatures (T_a) in newborns but less so in older animals. The decline occurred even though MR increased. Jackrabbits 79-82 days-old maintained a relatively constant rectal temperature (T_{re}) between 0 and 25 °C. Homeothermy development was associated with an increased cold tolerance and a decline in the absolute values of the slopes $\Delta MR / \Delta T_a$ and $\Delta T_{re}/\Delta T_a$ with age. Regression equations were derived to describe MR and T_{re} in 4-81 day-old white-tailed jackrabbits at air temperatures of 0-25 °C.

INTRODUCTION

The development of homeothermy may vary among leporids because some, such as the rabbit (<u>Oryctolagus cunniculus</u>), are altricial, while others, e.g., <u>Lepus</u> spp., are more precocial. Altricial offspring show a delay in the attainment of independent activity and self-maintenance, compared to precocial offspring (Lincoln et al. 1982). Newborn rabbits have much less mobility and develop pelage later than <u>Lepus</u> spp. The eyes are also closed at birth in rabbits, as opposed to open in <u>Lepus</u> spp. (Kanable 1977; pers. observ.). The energetics of homeothermy development in precocial and altricial mammals has been reviewed (Hull 1973, Alexander 1975, Blix and Steen 1979). In general, precocial newborns have better pelage insulation, maintain a higher body temperature as the air temperature declines, and need to generate less metabolic heat at low air temperatures than altricial newborns.

The ontogeny of homeothermy has been described in the rabbit (Dawkins and Hull 1964; Hull 1965; Farkas et al. 1972a,b) but not in *Lepus* spp. The purpose of this study was to examine the metabolic and body temperature changes occurring with neonatal growth in white-tailed jackrabbits (*Lepus townsendii*) for comparison with the altricial rabbit. I found that jackrabbits and rabbits have many similarities in their thermoregulatory development, which would not be expected by assessing the degree of precociality by physical appearance.

METHODS

White-tailed jackrabbits were trapped in Sweetwater County, Wyoming, during Autumn, 1987, and held in large, outdoor pens at the Green Canyon Ecology Compound, Utah State University, Logan, Utah. Three pairs of adult jackrabbits mated in captivity and produced offspring during the spring and summer, 1988. The birth dates of the young were estimated to the nearest day. Lactating does and weaned leverets (at about 30 d) were supplied *ad lib*. with commercial rabbit pellets (16% crude protein, 2 % fat, and 17% crude fiber), apples, and alfalfa.

Energetics experiments were conducted during the daytime (the inactive phase for jackrabbits) with young jackrabbits fasted >10 hr. I used an 18 l metal, metabolism chamber that had its inside walls painted flat black to reduce reflection (cf. Porter 1969). An animal was placed onto a wire grid suspended 2 cm above the chamber floor to minimize conduction between it and the chamber. Air temperature (T_a) in the chamber was regulated to ± 1 °C and monitored with two thermocouples (Wescor).

Air was pumped from the sealed chamber at 6 l/min and the O_2 content of a fraction of dry, CO_2-free air was analyzed (S-3A, Applied Electrochemistry). The flow temperature was measured by thermocouple and the atmospheric pressure was measured by barometer. The rate of oxygen consumption ($\dot{V}O_2$) was then calculated at STP using Equation 2 in Hill (1972) and converted to metabolic rate (assuming 19.67 $kJ \cdot (l\ O_2)^{-1}$). The rectal temperature (T_{re}) of a jackrabbit was determined on a separate day to avoid disturbance to animals while recording O_2 content. T_{re} was measured until a constant temperature was reached with a 16 ga thermocouple wire inserted 2.5 cm into the rectum. Metabolic rates and body temperatures of juveniles were compared with those of adults (see Chapter VI).

Oxygen consumption and body temperature were each determined at air temperatures of 0, 5, 10, 15, 20, and 25 °C for 60 min, with 60 min between measurements. T_a was increased between $\dot{V}O_2$ determinations (n = 11 animals). T_a was increased (n = 10 animals) or decreased (n = 8 animals) between T_{re} determinations. All T_{re} measurements were pooled because rectal temperatures were similar if T_a was raised or lowered (P = 0.18). Jackrabbits were usually inactive in the metabolism chamber. Trials in which animals were active were omitted from the analysis.

RESULTS

The metabolic rate (MR) was highest in 4-5 day old jackrabbits, approximately 50% lower at 9-14 days, and lowest in older animals (Fig.

14). The metabolic rate of 80-81 day-old jackrabbits (4.4 ± 0.24 W/kg; mean ± SE) was still higher ($\underline{P} < 0.001$) than that of adults (2.82 ± 0.30 W/kg). These trends were most pronounced if data were expressed per kg rather than $kg^{0.75}$ (Fig. 14a, b). However, the difference in MR among age groups was significant with either scaling factor ($\underline{P} < 0.001$).

The slope, $|\Delta MR/\Delta T_a|$ (units = $W\cdot(°C\cdot kg)^{-1}$) declined with age ($\underline{P} < 0.001$). The mean slope for T_a between 0 and 25 °C was 0.50 ± 0.020 at 4-5 days, 0.25 ± 0.009 at 9-14 days, 0.12 ± 0.005 at 27-34 days, and 0.04 ± 0.003 at 54-81 days.

The rectal temperature (T_{re}) also differed ($\underline{P} < 0.001$) between age groups and was higher in the older animals (Fig. 15). The rectal temperature declined with lower T_a in jackrabbits less than 79-82 days-old. The slope $|\Delta T_{re}/\Delta T_a|$ was steepest in the youngest animals ($\underline{P} < 0.001$), 0.16 ± 0.007 at 4-15 days, 0.06 ± 0.005 at 33-34 days, and 0.004 ± 0.003 at 79-82 days for T_a between 0 and 25 °C.

Curves were fit to the metabolic and body temperature data using least squares estimation. The two regression models that explained the most variance for all animals are shown, where age is in days:

$MR\ (W/kg) = \exp(3.9 - 0.017\cdot T_a - 0.51\cdot \ln[age])$, $\underline{R}^2_a = 0.88$

$T_{re}\ (°C) = 27.8 + 2.28\cdot \ln(age) + 0.25\cdot T_a - 0.05\cdot \ln(age)\cdot T_a$, $\underline{R}^2_a = 0.70$. Because of the large difference in MR between 4-5 day-old and older white-tailed jackrabbits, best fit equations were also derived for these groups. For jackrabbits 4-5 day-old:

$MR\ (W/kg) = 39.6 - 0.43\cdot T_a - 2.73\cdot Age$, $\underline{R}^2_a = 0.92$. For jackrabbits 9-81 days-old:

$MR\ (W/kg) = 18.9 - 0.090\cdot T_a - 3.09\cdot \ln(Age)$, $\underline{R}^2_a = 0.80$

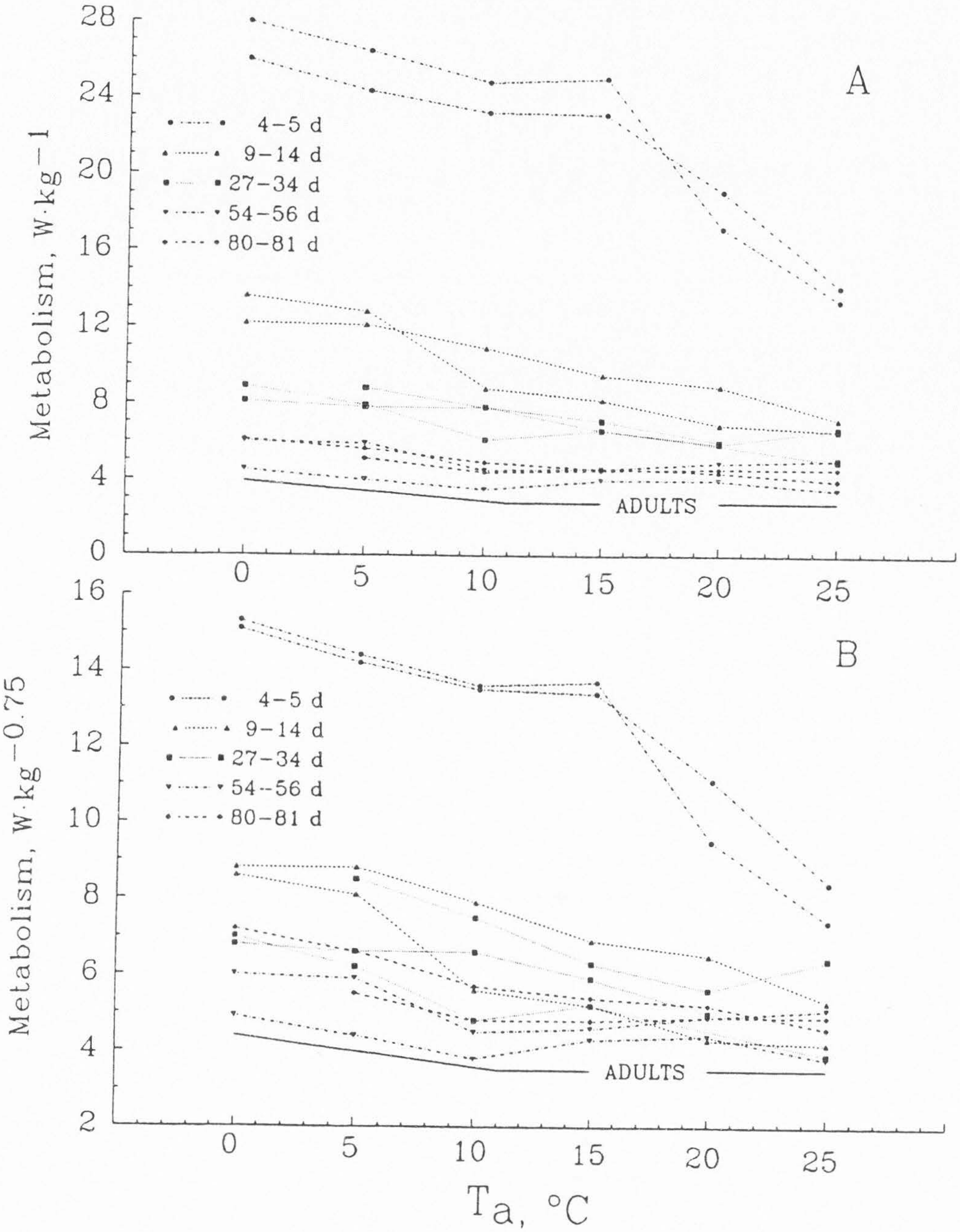

Fig. 14. Metabolic rates of juvenile white-tailed jackrabbits expressed as W·kg^{-1} (A) and W·kg$^{-0.75}$ (B) ($\underline{n}$ = 11 animals). The average metabolic rate of summer-acclimatized, adult jackrabbits is shown for comparison.

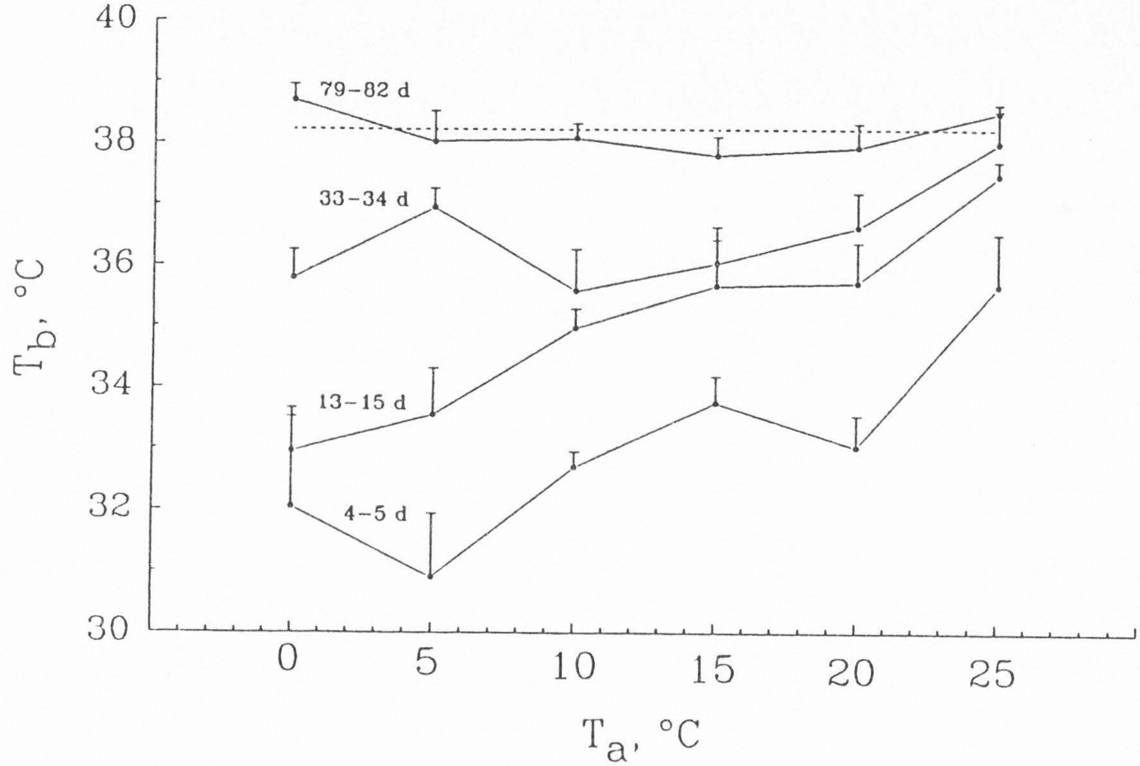

Fig. 15. Rectal temperatures of juvenile white-tailed jackrabbits (mean ± SE; n = 6 animals at 33-34 days, 4 otherwise). The average body temperature of summer-acclimatized, adult jackrabbits is shown (dashed line) for comparison.

DISCUSSION

White-tailed jackrabbits were expected to conform to the developmental pattern of precocial endotherms, with normothermy and a metabolic rate similar to adults attained at an early age (cf. Hull 1973, Alexander 1975). However, the variation in body temperature and energy metabolism in newborn jackrabbits was similar in many ways to that found in altricial species. At low air temperatures (T_a), the newborns had a much higher metabolic rate and a lower body temperature than adults, which might be expected in animals with poorly developed insulation and substantial heat loss to the environment.

Even though newborn white-tailed jackrabbits were covered with fur, the metabolic rate (MR) of 4-5 day-old jackrabbits at 0 °C, 27 ± 1.4 W/kg, was almost twice that at 25 °C, 14 ± 0.7 W/kg. Newborn rabbits (_O. cunniculus_), which are altricial, also have a large capacity to elevate their O_2 consumption at low T_a (Dawes and Mestyán 1963). Non-shivering thermogenesis (NST) in brown adipose tissue probably accounts for the capacity to increase the metabolic rate at low T_a (Dawkins and Hull 1964, Hull and Segall 1965). Brown fat and NST are important in the cold metabolism of both _Lepus_ and _Oryctolagus_ species (Heldmaier 1971, Feist and Rosenmann 1975, Kolodeznikova and Afanasiev 1980).

In newborn rabbits, the body temperature drops with lower T_a despite increased metabolic heat production (Hull 1965, Farkas et al. 1972a). Similarly, the rectal temperature (T_{re}) of newborn jackrabbits declined at lower T_a even though their metabolic rate increased. Farkas et al. (1972a) have suggested that newborn rabbits might regulate their body temperature at a low temperature. The benefit of the hypothermia could be a reduction in heat loss at cold air temperatures because of a lower temperature difference, T_{re} - T_a. It is unknown whether newborn jackrabbits regulate body temperature at a lower level than that of adults. However, the large variation in T_{re} (Fig. 15) suggests that they do not control body temperature precisely.

The metabolic rate was significantly lower in older than in young white-tailed jackrabbits. An age-dependent decline in metabolic rate has also been reported in rabbits (Hull 1965; Farkas et al. 1972a,b). Reduced metabolic rate in older animals is related to a decrease in NST and an increase in shivering thermogenesis as the muscle mass develops (Scopes and Tizard 1963, Hull 1973). Thermogenic capacity may decline because a smaller increase in oxygen consumption at low T_a is induced by shivering than by NST (Brück and Wünnenberg 1965).

In white-tailed jackrabbits, improved cold tolerance was indicated partly by a lower metabolic rate and a more gradual slope of MR on T_a in older animals. These changes were marked because the metabolic rates of 4-5, 9-14, and 27-34 day-old jackrabbits at T_a = 0 °C were approximately 4, 2, and 1.5 times that of 54-81 day-old animals, respectively (Fig. 14). Declines in the slopes of metabolic rate and body temperature with T_a suggested that the insulation and resistance to heat loss improved with age. The lower slope of body temperature decline was not caused by greater heat production at low T_a because the increase in metabolism with lower T_a was least in the oldest animals.

In conclusion, the developmental pattern of white-tailed jackrabbits is similar to that of altricial rabbits (Hull 1965, 1973). Following the initial reduction in metabolic rate, which appears due to a greater reliance on shivering than non-shivering metabolism with age, tolerance to cold air temperatures develops gradually. Older animals in both species have a higher and steadier body temperature, a lower metabolic rate, and a less marked increase in the metabolic rate with lower air temperature.

The only apparent difference between the rabbit and the white-tailed jackrabbit is that the latter has a higher rate of oxygen consumption. The oxygen consumption of 4-5 day-old rabbits reaches a plateau at 19 W/kg at 20°C (Hull 1965; assuming RQ = 0.8). In comparison, the metabolic rate of white-tailed jackrabbits of the same age increased from 18 ± 0.9 W/kg at 20 °C to 27 ± 1.0 W/kg at 0 °C.

CHAPTER VIII

INFLUENCES OF AIR TEMPERATURE, WIND, AND RADIATION ON ADULT METABOLISM

Low air temperatures and high wind speeds elevated the metabolic rate of jackrabbits (Lepus townsendii) in summer and winter, but the greatest metabolic increase was in summer. Regression equations derived by the method of least squares described 90% of air temperature and wind effects on metabolism. The best fit regression models included an air temperature-wind interaction each season, linear terms for wind in summer, and non-linear terms for wind in winter. Jackrabbit body temperature also increased with wind, apparently because metabolic heat production overcompensated for convective heat loss. Wind effects on free-living jackrabbits were most probable during the winter (when highest wind speeds occurred). Incident radiation can lower winter energy use. The metabolic rate was reduced with irradiation (0.3-2.8 m) at air temperatures below the lower critical temperature (LCT) in winter. No effect of irradiation on metabolic rate was detected below LCT in summer or above LCT in either season.

INTRODUCTION

The influence of air temperature on metabolic rate has been documented for white-tailed jackrabbits and other Lepus species (see Chapter VI) but effects of air temperature, wind, and radiation on metabolic rate have not been reported. Effects of these variables on metabolism have been described empirically only for raptors (Hayes and Gessaman 1980) and one sciurid species (Neal 1976). High mortality during winter storms (Stoddart 1985) suggests that wind has a large influence on thermoregulatory energy use by jackrabbits. Forced convection reduces thermal resistance and increase heat flow through pelage (Moote 1955, Lentz and Hart 1960, Tregear 1965). Heat production increases with wind at low ambient temperatures in pigs (Close et al. 1981), caribou (Hart et al. 1961), sheep (Joyce and Blaxter 1964), and other ungulates (see Chappel and Hudson 1978). Higher heat production replaces heat lost by forced convection in a cold environment to maintain a thermal equilibrium.

Incident radiation (irradiation) can decrease thermoregulatory energy use by endotherms at air temperatures below the lower critical temperature or increase it as air temperatures approach the upper critical temperature (Hamilton and Heppner 1966, Lustick 1969, Neal and Lustick 1975, DeJong 1976). In desert lagomorphs, resting under vegetation may reduce the radiative heat gain during mid-day or loss at night (Schmidt-Nielsen et al. 1965, Hinds 1973, 1977). Black-tailed jackrabbits (L. californicus) have been observed lying in the morning sunshine (Costa et al. 1976), which could reduce metabolic cost at low air temperatures. Interactions of wind, radiation, and heat transfer through fur or feathers have been reported in several endotherms (Hutchinson and Brown 1969, Cena and Monteith 1975, Walsberg et al. 1978) but their implications for metabolic heat production in Lepus species have not been evaluated.

I conducted controlled experiments to quantify the simultaneous effects of air temperature, wind speed, and irradiation on the metabolism of white-tailed jackrabbits (L. townsendii). The energy requirement in the field was evaluated based on this metabolism study and micrometeorological measurements in natural habitat. White-tailed jackrabbits are nocturnal and rest during the daylight in forms (shallow depressions they dig in the soil beneath shrubs or other vegetation). Daytime wind and solar radiation are reduced at the form (Flinders and Elliot 1979). Exposure to wind should be greatest at night when animals are active.

METHODS

Oxygen consumption and core body temperature were measured in six jackrabbits (three of each sex) during July-August, 1986 and January-February, 1987. The jackrabbits were trapped in Sweetwater County, Wyoming, housed outside in pens at the Green Canyon Ecology Compound, Utah State University, Logan, UT, and fed commercial rabbit chow supplemented with alfalfa and apples. Energetic experiments were conducted during daylight hours with animals fasted overnight (>10 hr).

Metabolic rate was determined using a closed-circuit wind tunnel (described by Rogowitz [1988]). Wind speed (U) was generated by a blower and controlled with a rheostat. A hot-wire anemometer (Weather Measure) was used to calibrate the wind speed. Air temperature (T_a) was changed by varying the air temperature of the environmental chamber in which the wind tunnel was placed. T_a was monitored by calibrated thermocouple with a thermocouple thermometer (Wescor). Jackrabbits were irradiated by lamps suspended 0.5 m above a window of UVT acrylic (Rohm and Haas) on the top of the wind tunnel. Irradiation was changed by varying the number of lamps turned on with a remote electrical switch. The spectrum of one lamp (General Electric, 250 W R40/1) before and after filtration by the window is shown (Fig. 16). The level of irradiance (R; W/m^2) on a jackrabbit was estimated using a wide-range pyranometer (Stern, 0.2- 2.8 m) placed 0.1 m above the chamber floor. An external fan was aimed at the acrylic window to prevent its warming and emitting long-wave radiation. The walls in the wind tunnel were painted flat black to reduce reflection (Porter 1969).

Oxygen in air pumped from the wind tunnel was analyzed (S-3A Analyzer, Applied Electrochemistry) after CO_2 and moisture were absorbed. Barometric pressure and flow temperature were measured with a mercury barometer and calibrated thermocouple, respectively. The rate of oxygen consumption was then calculated at STP with Equation 2 in Hill (1972) and converted to $W/kg^{0.75}$ (assuming 19.67 $kJ \cdot (l\ O_2)^{-1}$). The oxygen content was measured for 90 min at randomly chosen levels of air temperature, wind speed and irradiance, with at least 60 min between measurements to allow adjustment for a change in conditions. The air temperature-wind effect on metabolism was measured at T_a = 2, 16, and 30 °C in summer, at -12, -5, 2, and 16 °C in winter, and at U = 0, 6, and 12 m/s during both seasons. The three-way effect (air temperature-wind-radiation) was measured at T_a = 2 and 16 °C, U = 0, 6, and 12 m/s, and R = 0, 133, and 400 W/m_2 in summer and at T_a = -12, 2, and 16 °C, U = 0 and 6 m/s, and R = 0, 540, and 1080 W/m^2 in winter. The mean body mass of jackrabbits was 2.43 ± 0.04 kg (mean ± SE) in summer and 2.81 kg ± 0.04 in winter experiments.

The body temperature of each jackrabbit was estimated from the pulse rate of an implanted transmitter (Minimitter) that was calibrated to ± 0.1 °C and sutured to the inner abdominal wall at the linea alba.

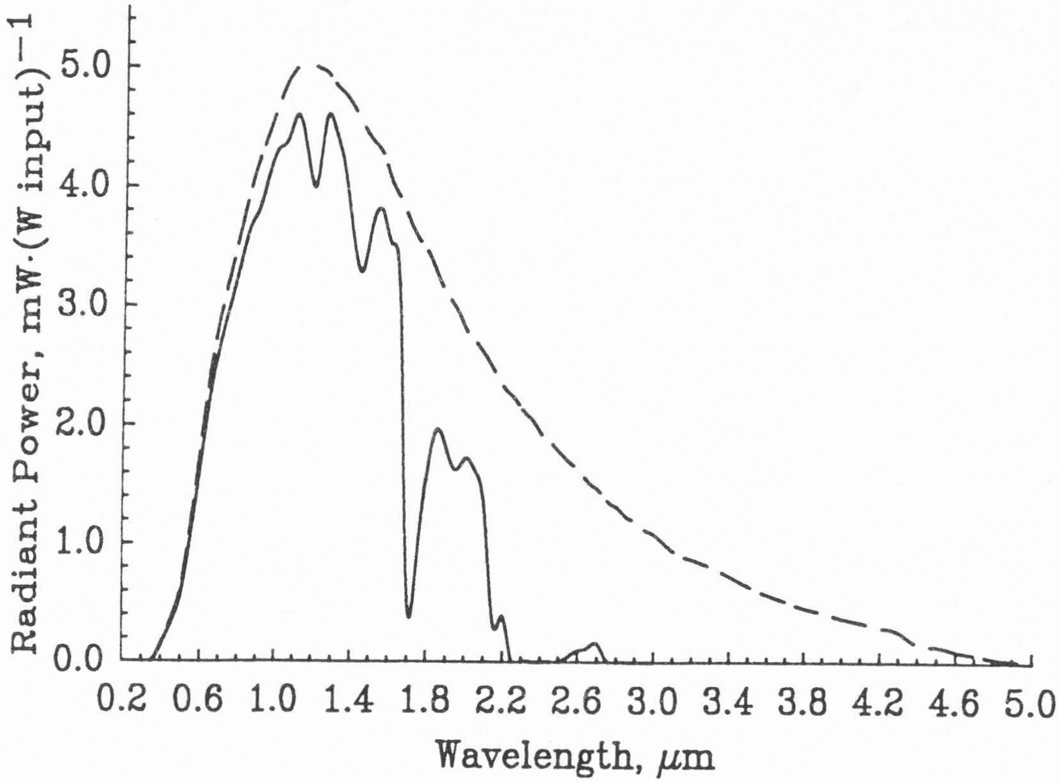

Fig. 16. Spectrum of one radiation lamp (GE, 250 W R40/1) before (dashed line) and after (solid line) passing through the wind tunnel window of UVT acrylic.

Transmitted signals were detected (by an antenna looped around the inside wall of the wind tunnel near the jackrabbit) and relayed to a remote AM receiver. Body temperatures was estimated three times each trial during steady periods of oxygen consumption.

Air temperature was monitored continuously with thermographs (in ventilated shelters) placed 0.2 m above ground level in Carter and 10 km NW of Carter, Uinta County, Wyoming. Wind speed was measured by cup anemometer at 0.2 m above ground level at Carter. Measurements with maximum/minimum thermometers and totalizing anemometers placed within 20 km of Carter were within the 95% confidence interval of ambient data from Carter. Therefore, only Carter data are shown. Air temperatures were taken from the chart record at 2 hr intervals; wind speeds were integrated over 1 hr periods. A FORTRAN program was written to computed means and errors of these variables over day and night hours for each day of year.

Wind profiles were developed for sagebrush (Atriplex tridentata) and adjacent, open grassland by measuring wind speed concurrently in both habitats at 0.05, 0.25, 0.5, 1.0, 1.5, and 2 m above ground level. Duct anemometers (Weathermeasure) were manually aligned perpendicular to the wind direction and wind measurements were integrated for 10 min. Air temperature was also measured concurrently between habitats with a standard mercury thermometer in a ventilated, reflective shelter.

Effects of ambient variables on metabolic rate or body temperature were tested with ANOVAs and t-tests. Least square regression was used to describe trends in the data.

RESULTS

The metabolic rate of white-tailed jackrabbits increased with wind at 16 and 2 °C in summer and at 2, -5, and -12 °C in winter (Fig. 17; $\underline{P} < 0.001$, $\underline{n} = 72$ each season). Air temperature and wind effects on metabolism interacted ($\underline{P} < 0.001$, $\underline{n} = 72$): the rate of metabolic increase was greater at lower air temperatures and higher wind speeds each season. The metabolic rate did not increase with wind applied at the warmest air temperature tested in summer, 30 °C, and winter, 16 °C. The rate of metabolic increase with low air temperatures and high wind speeds was greater in summer than in winter. At a wind speed of 12 m/s, metabolic rates at 2 °C in summer and -12 °C in winter were similar.

Least squares regression was used to derive equations to describe effects of air temperature and wind on the metabolic rate (Table 8). Regression equations that included a term for the air temperature-wind interaction had the least residual variance each season. Equations with linear wind components described the air temperature-wind interaction most closely in summer. Curves with non-linear components (ln [wind] or $\text{wind}^{0.5}$) described the effect best in winter. However, The log relationship is not defined at $U = 0$ m/s.

The lower critical temperature (LCT) of white-tailed jackrabbits in calm air declined from 11 °C to -6 °C from summer to winter (Chapter VI). In winter, the metabolic rate was lower ($\underline{P} = 0.01$, $\underline{n} = 36$) for irradiated than non- irradiated animals at $T_a <$ LCT ($T_a = -12$ °C) irrespective of wind speed (Fig. 18). There was no significant irradiation effect ($\underline{P} > 0.05$) on the rate of metabolism below LCT in

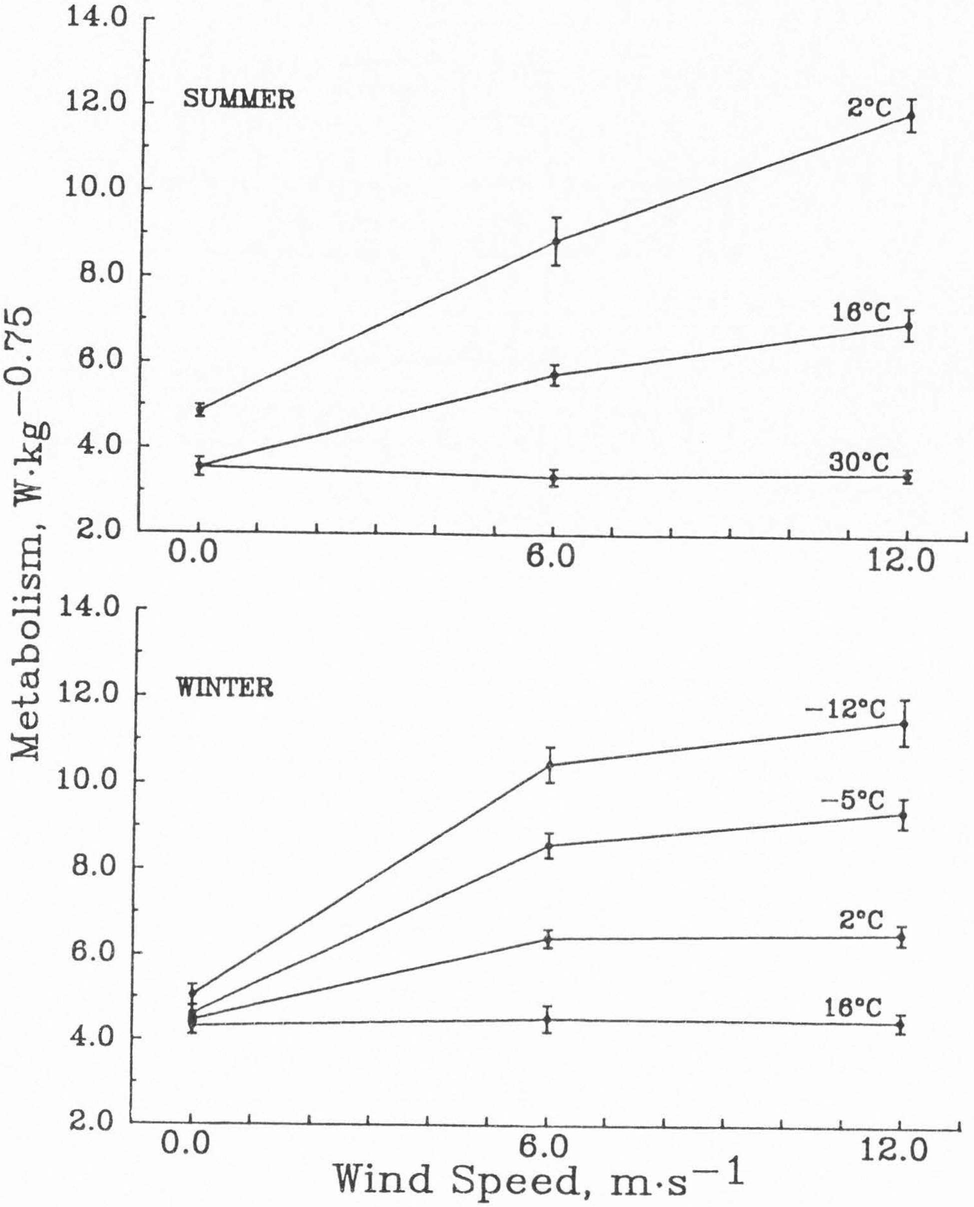

Fig. 17. Effects of air temperature and wind speed on jackrabbit metabolism in summer and winter (mean ± SE).

Table 8. Regression models of air temperature (T) and wind speed (W) effects on the metabolic rate of white-tailed jackrabbits in summer and winter. Coefficients for model components are listed in order next to the regression constant. the coefficient of multiple determination, R^2_a, and *F*-test values are reported.

Model Components	Model Parameters Constant	1st	2nd	3rd	R^2_a	*F*
Summer						
T,W	6.99	-0.182	0.291		0.75	82.2
T,$W^{0.5}$	6.82	-0.182	0.975		0.75	81.1
T,ln(W)	8.79	-0.182	0.422		0.73	71.6
T,W,TxW	4.95	-0.054	0.631	-0.023	0.93	233.6
T,W,Tx$W^{0.5}$	4.56	-0.041	2.120	-0.071	0.92	221.4
T,ln(W),Txln(W)	8.84	-0.185	0.919	-0.031	0.88	136.5
Winter						
T,W	5.05	-0.163	0.281		0.69	80.8
T,$W^{0.5}$	4.74	-0.163	1.010		0.73	98.5
T,ln(W)	6.79	-0.163	0.467		0.74	102.2
T,W,TxW	5.02	-0.048	0.286	-0.019	0.83	118.4
T,W,Tx$W^{0.5}$	4.71	-0.029	1.030	-0.068	0.89	193.8
T,ln(W),Txln(W)	6.79	-0.166	0.475	-0.031	0.90	215.8

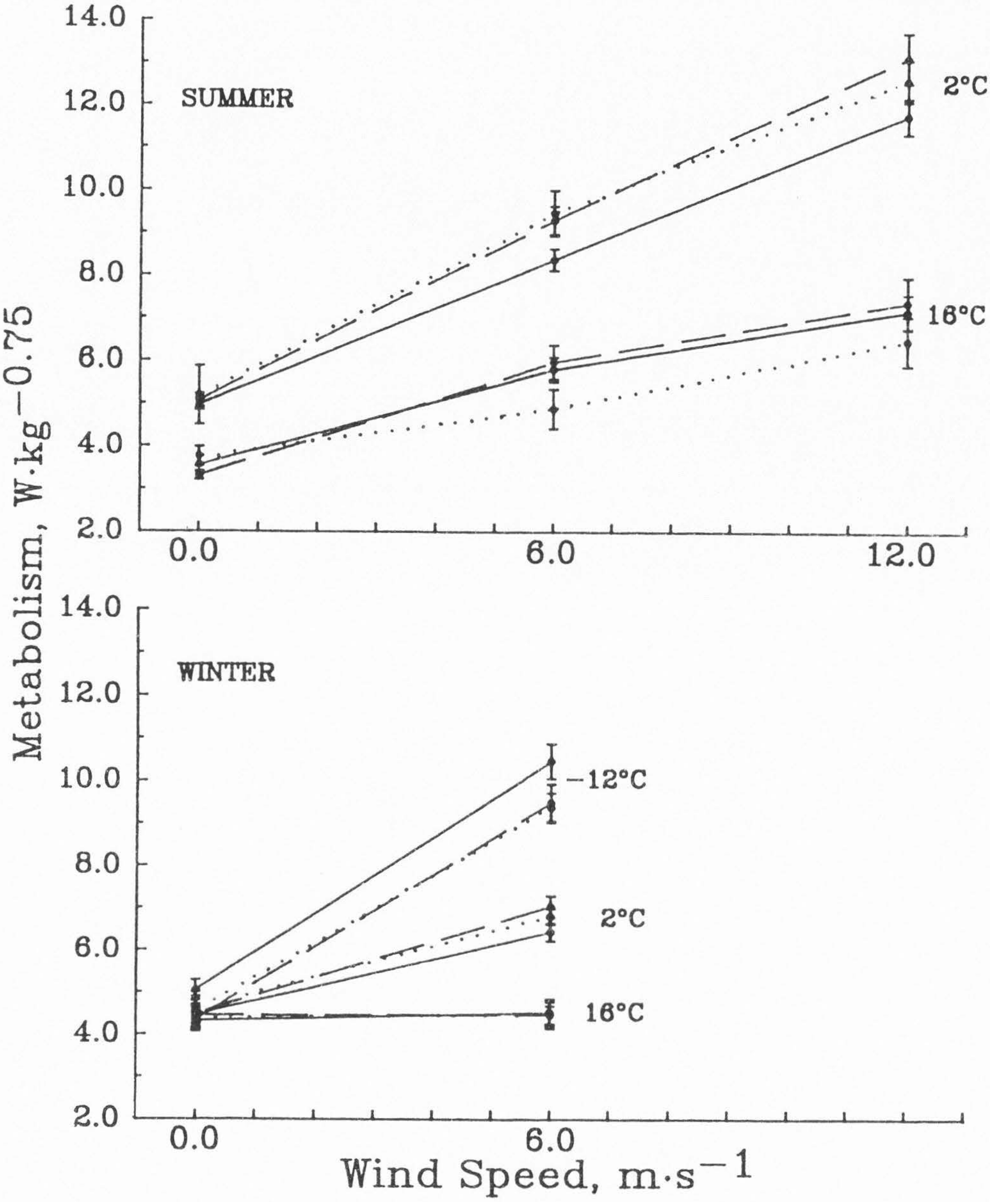

Fig. 18. Influences of air temperature, wind speed, and irradiation on jackrabbit metabolism in summer and winter (mean ± SE). The level of irradiance was 0 W/m^2 (solid line), 133 W/m^2 (dashed line), and 400 W/m^2 (dotted line) in winter and 0 W/m^2 (solid line), 540 W/m^2 (dashed line), and 1040 W/m^2 (dotted line) in summer.

summer. Irradiation also had no significant effect ($\underline{P} > 0.05$) on the metabolic rate above the LCT in either season.

In calm air, body temperatures of white-tailed jackrabbits were stable over a wide range of T_a and higher in winter than in summer (Chapter VI). Body temperature (T_b) increased with wind ($\underline{P} < 0.01$, $\underline{n} = 72$) during winter, $T_b = 39.0 \pm 0.29$ °C (mean ± SE), 39.2 ± 0.05 °C and 39.3 ± 0.06 °C at U = 0, 6 and 12 m/s, respectively. The body temperature change between the same wind speeds was non-significant ($\underline{P} > 0.05$) in summer, 38.2 ± 0.07 °C, 38.3 ± 0.11°C and 38.3 ± 0.11, respectively. An effect of irradiation on T_b was not detected in winter ($\underline{P} = 0.355$, $\underline{n} = 108$) and was not tested in summer.

Wind speeds in southwestern Wyoming were higher during the days than the nights, higher in winter than in summer, and extremely variable (Fig. 19). At heights ≤ 0.5 m above ground level, higher wind speeds were recorded in open habitat than in adjacent sagebrush habitat (Fig. 19, inset). At 0.05 to 0.25 m above ground level, space occupied by the jackrabbit, the wind speed was 40% greater in open areas than in sagebrush habitat. Air temperatures did not differ between sagebrush and adjacent open sites. Mean daytime and nighttime air temperatures (T_a; °C) in the habitat of jackrabbits during 1985-87 were fit to cosine curves using the SIMPLEX algorithm for non-linear estimation (Caceci and Cacheris 1984): Mean daytime $T_a = 7.7 + 13.73 \cdot \mathrm{COS}(0.0172 \cdot [\mathrm{Day} - 194])$ ($\underline{R}^2 = 0.79$, SE = 0.15). Mean nighttime $T_a = 0.5 + 10.96 \cdot \mathrm{COS}(0.0172 \cdot [\mathrm{Day} - 198])$ ($\underline{R}^2 = 0.75$, SE = 0.13); where Day = day of year (1-365).

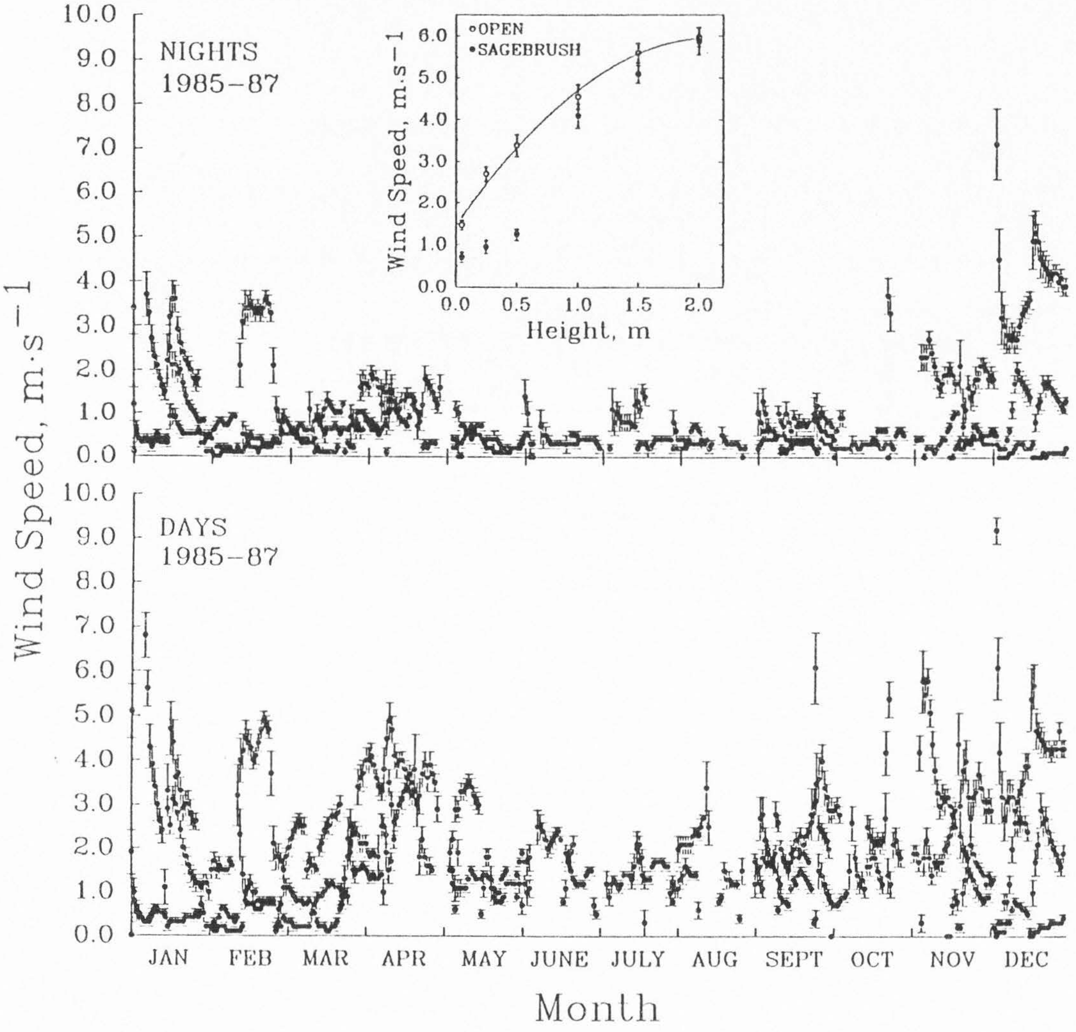

Fig. 19. Daytime and nighttime wind speeds (mean ± SE) at 0.2 m above ground level, Carter, Wyoming, 1985-1987. Inset shows wind profiles taken simultaneously at each height above ground level in sagebrush and adjacent open habitat.

DISCUSSION

The thermal budget of an animal is complex and involves terms for metabolic heat production, sensible and insensible heat fluxes, work and heat storage. The sum of these components must equal zero to achieve a thermal equilibrium (Gates 1980). Harris et al. (1985) found that wind increases heat conductance through black-tailed jackrabbit pelts and that this effect is greatest in summer pelts. Similarly, in summer, when the overall thermal conductance of white-tailed jackrabbits was highest (Chapter VI), the rate of increase in metabolic heat production with wind was highest. The higher metabolic heat production in summer appears to compensate for the greater heat loss.

Heat loss is a function of thermal conductance and the temperature gradient between an animal and its environment. The higher summer conductance could increase the surface temperature (T_s), the temperature gradient (T_s - T_a), and the heat loss at air temperatures below the surface temperature. Indeed, the metabolic rate with a high wind speed (12 m/s) was greater at T_a = 2 °C in summer than winter. Wind elevated the metabolic rate at 16 °C in summer but not winter. At 30 °C in summer and 16 °C in winter, wind did not increase metabolism, which suggests that the body surface and air temperatures were equivalent at these T_a.

Air temperature and wind had an interactive influence on the metabolic rate of jackrabbits. The increase in metabolic rate was greatest when jackrabbits were exposed to the lowest air temperatures and the highest wind speeds. Equations that included the significant temperature x wind interaction described approximately 90% of variance in metabolic rate (Table 8). When the interaction was omitted from the regression model, much less variance was explained.

The metabolic rate increased linearly with wind speed in summer, but the relationship was nonlinear in winter. The rate of increase in metabolism declined with higher wind speeds in winter. Exposure to low wind speeds is sufficient to disrupt insulation in rabbits (Tregear 1965) and better insulated ungulates (Hofmeyr 1985). Thus, the slight non-linearity in winter appears unrelated to wind penetrance into the pelage. The more heavily furred winter-acclimatized animals may be better able to reduce the rate of heat loss at higher wind speeds by postural changes.

The metabolic rate declined with irradiation in white-phase winter animals but not in the brown-phase summer animals. The difference may be due to radiation dosage. A significant reduction was found at 540 and 1080 W/m^2 in winter but not at $\leq$ 400 W/m^2 in summer. Most of the radiation is absorbed on the surface in animals with dark coats (Hutchinson and Brown 1969, Finch et al. 1980) but the penetrance is deeper into white coats, particularly with wind (Walsberg et al. 1978). A short white fur growing from a dark skin will trap solar radiation effectively (Cena and Monteith 1975). Jackrabbits have dark skins, brown fur in summer, and white fur with tawny-colored bands mid-shaft in winter. The lower metabolic rate with radiation in winter suggests that penetrance of the radiation was greater into white winter pelage than brown summer pelage.

The body temperature of white-tailed jackrabbits increased at higher wind speeds. Since the oxygen record increased gradually, and was not erratic, the greater energy use was not due to increased movement. An increase in body temperature with wind has also been reported in studies with sheep (Alexander 1961, Joyce and Blaxter 1964). A higher body temperature may occur if metabolic heat production overcompensates for convective heat loss. This suggests that animals may have been stressed at high wind speeds. In natural habitats, jackrabbits may avoid very high winds by moving into sheltered areas (Tiemeier 1965, Stoddart 1985), which is not possible in a metabolism chamber. Vegetation can shield white-tailed jackrabbits from high wind speeds occurring during the daytime (Fig. 19). Jackrabbits are active at night (Fig. 10), when wind speeds are usually lower.

Because the highest wind speeds occurred during winter (Fig. 19), the greatest possible effect of wind on thermoregulatory metabolism in wild animals was during that season. Severe winds may induce or contribute to high mortality in black-tailed jackrabbits during winter storms (Stoddart 1985).

CHAPTER IX

JACKRABBIT POPULATION ENERGETICS MODEL

A computer model was developed using empirical data to estimate population energy expenditure for white-tailed jackrabbits in semi-desert habitat in southwestern Wyoming. Metabolizable energy requirements for maintenance, thermoregulation, activity, reproduction, and growth were estimated. The energy requirement ($kJ \cdot kg \cdot day^{-1}$) was greatest for juveniles at birth, adult females during lactation, and adult males during the breeding season onset. Winter was not the most energy-demanding season because adult thermoregulatory cost was low. Juveniles comprised most of the population biomass in spring and summer and consumed the most energy per year. The energy expenditures for adult males, adult females, juveniles, and all animals in the population were 130, 191, 224 and 546 $MJ \cdot individual^{-1} \cdot km^{-2} \cdot yr^{-1}$, respectively. Air temperatures <4 °C and higher wind speeds at 0.2 m above ground level increased population energy expenditure. Simulated huddling reduced juvenile energy expenditure. Jackrabbits were estimated to consume only a small fraction of above-ground phytomass energy and were not likely to be food limited in the semi-desert area. Estimated percent consumption of forage energy was 4%, assuming only 50% of phytomass was edible, population density = 100 jackrabbits/km^2, metabolizable energy efficiency = 0.4, and calm air.

INTRODUCTION

The requirement of populations of hares (*Lepus* spp.) for energy in primary production is complex and not fully understood. Keith et al.

(1984) have suggested that food limitation initiates periodic declines in populations of snowshoe hares (*L. americanus*). They reported a pattern of reduced body mass, delayed breeding, and increased juvenile mortality in high density populations (see also Keith and Windberg 1978, Pease et al. 1979, Vaughan and Keith 1981). Similarly, low availability of winter food is associated with reduced body mass, high mortality, and subsequent population decline in an island population of mountain hares (*L. timidus*) (Angerbjörn 1981). In contrast, models of forage use by black-tailed jackrabbits (*L. californicus*) do not support the food limitation hypothesis (Clark and Innis 1982, Harris 1984).

Small mammals usually consume <10% of the annual, above-ground primary production (Chew and Chew 1970, Ryszkowski and French 1982). However, much of the production is not available to herbivores. Several factors including plant structure (Crawley 1983) and snow depth (Keith 1983) influence phytomass availability. Plant palatability also affects intake and assimilation of forage (Bryant and Kuropat 1980). Reduced availability of palatable food might constrain population growth in snowshoe hares (Bryant 1981, Fox and Bryant 1984). Information on the effect of a reduction in palatable forage on potential food limitation is lacking for other *Lepus* species.

I studied the population energetics of white-tailed jackrabbits (*L. townsendii*) in semi-desert habitat to provide data on their energy and forage requirements. Specific objectives were to estimate (1) seasonal energy expenditures and the periods of highest energy use in age-sex classes of jackrabbits (2) the amount of energy in the standing crop and in edible forage consumed by a jackrabbit population.

A model of population energy expenditure was written based on empirical information presented in the previous chapters and published in the literature. The model simulated the requirements of juvenile and adult jackrabbits for metabolizable energy. Daily energy expenditures for maintenance, thermoregulation, activity, growth, and reproduction and the periods of highest energy use were estimated. Population energy expenditure was then compared with the energy available in the standing crop.

Percent consumption of phytomass energy was estimated for two hypothetical scenarios. In the first case, I assumed all above-ground vegetation was available for consumption to estimate the fraction of phytomass energy consumed by jackrabbits. In the second case, only a portion (i.e., 50%) of above-ground vegetation was assumed to be available. This condition was required to evaluate whether phytomass is potentially limiting because much of range forage is inaccessible or unpalatable to herbivores (Bryant and Kuropat 1980, Crawley 1983). Indeed, jackrabbits are highly selective feeders and do not consume all portions of plants (Bear and Hansen 1966, Currie and Goodwin 1966). Both analyses included an examination of the effect of changes in jackrabbit population density on the consumption of phytomass energy because jackrabbit density can fluctuate markedly (Mohr and Mohr 1936, Kline 1963, Dumke 1973, Schwartz 1973). I also examined the influence of change in metabolizable energy efficiency on phytomass energy consumption because the amount of food jackrabbits require would increase with a lower efficiency.

GENERAL EQUATION OF THE MODEL

The energetic components of the model were primarily additive:

$$E = \sum_{i=1}^{365} \sum_{j=1}^{3} N \cdot B \cdot ([M, TR, SDA] + P + A + R + H) - L$$

E = total yearly population energy (kJ/km^2), i = day of year; j = age-sex class (adult male, adult female, juvenile); N = population density ($animals/km^2$) and B = biomass (kg/animal). Energy terms in parenthesis are mass-specific (kJ/kg): M = basal metabolic rate, TR = energy of thermoregulation, SDA = specific dynamic activity (heat increment of feeding), P = production energy (non-reproductive), R = energy of reproduction, A = activity energy, and H = heat loss due to system inefficiencies. The components M, TR, and SDA are estimated together because SDA reduces thermoregulatory cost above basal level (refer to subroutines described below). L = energy in milk from lactating females (kJ/km^2). Because juvenile energy demand is fueled initially by energy in milk, not by energy in phytomass, the juvenile energy demand supplied by milk energy (L) is deducted from the total.

Reproductive energy (R) includes only gestation and lactation costs of adult females. Juveniles do not reproduce (Chapter III). The cost of gonadal production is negligible in adult males because testes mass increases by only 20 g in the breeding season, which is <1% of body mass. Energy of pelage production is ignored in the model because fur comprises <3% of body mass. Also, the daily cost of molt is small because the molt period is approximately 7 weeks.

MODEL STRUCTURE

The model, entitled ENERJACK, was written in FORTRAN 77 and runs on a Digital VAX computer. The code was written to be compatible other compilers, e.g., Microsoft FORTRAN. Extensive comments at the beginning of each program segment explain the FORTRAN code structure and function (see Appendix).

The model has a 3-tiered, logical hierarchy (Fig. 20). For each day of year, the main program calls second-tier subroutines which compile data for adult males, adult females, or juveniles. Second-tier subroutines call third-tier subroutines that calculate population growth and specific energy costs. The information then transfers back to the second tier where energy costs are summed per kg, per animal, and per all animals in an age-sex class. Energy demand per age-sex class is returned to the main program and summed to determine population energy demand per km^2.

Main Program

The main program prompts the user to set the pre-breeding density (animals/km^2) and initializes computations for each day of the year beginning on day 65 (6 March), the start of the breeding season. Daily and nightly air temperatures (T_a; °C) at 0.2 m above ground level are generated using cosine curves derived from mean daytime and nighttime T_a during 1985-87 (Fig. 21). Daytime and nighttime wind speeds (m/s) are inputed by the user to evaluate wind influences on energetic cost. Radiation effects are not simulated in ENERJACK because jackrabbits avoid high radiant temperatures by seeking shade (Schmidt-Nielsen et al. 1965, Hinds 1977) and radiation has only slight effects on metabolic

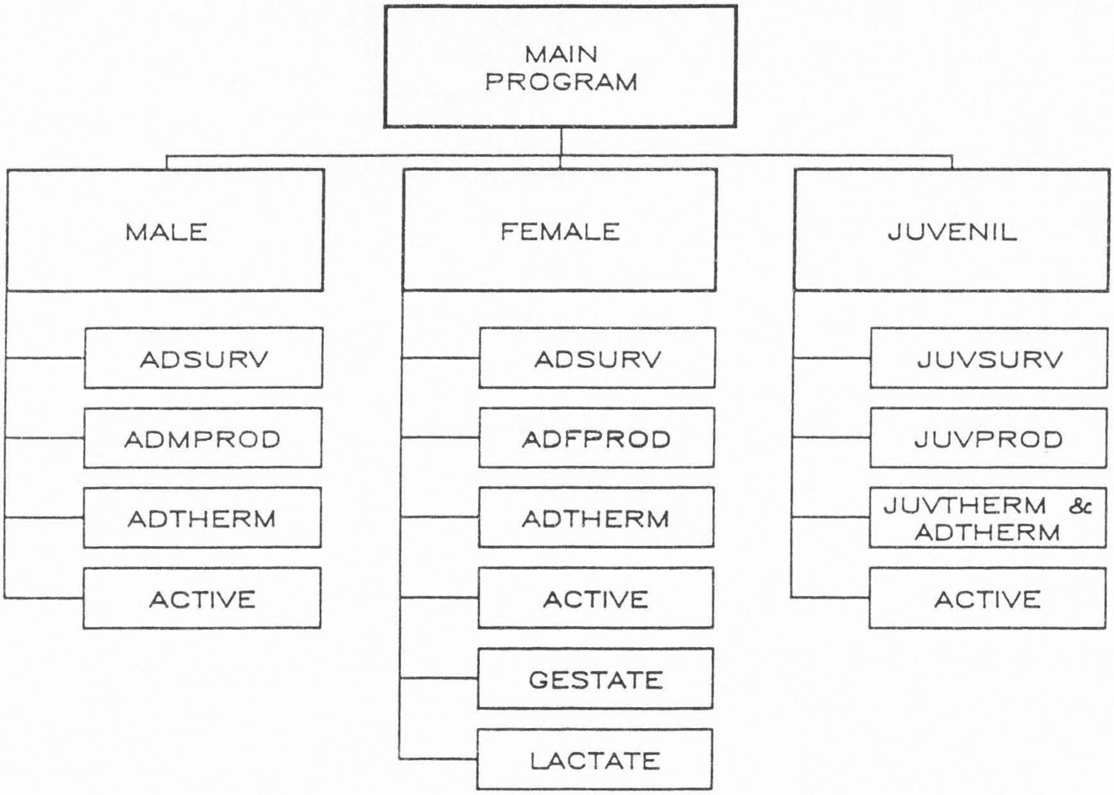

Fig. 20. Hierarchical structure of model ENERJACK.

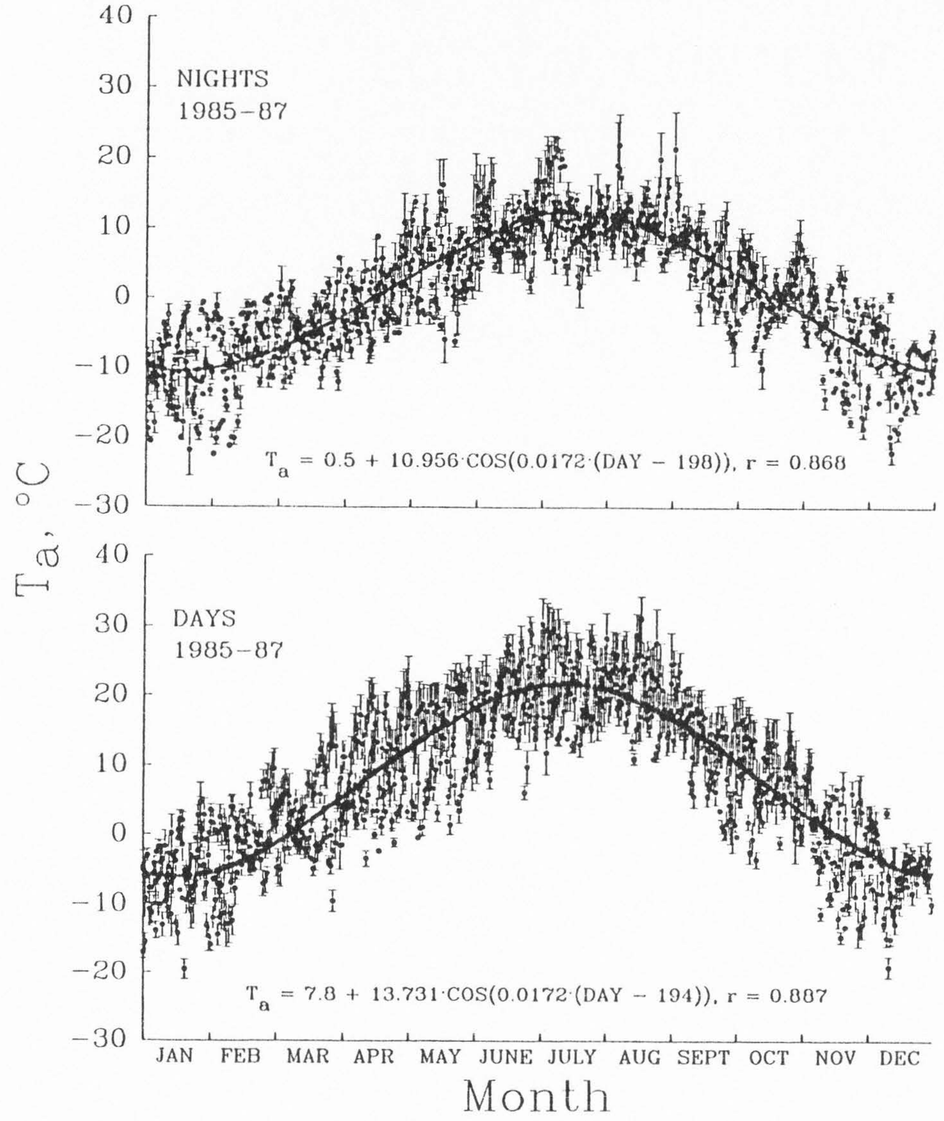

Fig. 21. Fit of cosine curves to mean daytime and nighttime air temperatures at 0.2 m above ground level during 1985-87.

rate at low air temperatures (Chapter VIII). If desired, the user can simulate energy savings by huddling of newborns (refer to "Maintenance and Thermoregulation" below). Daylength is calculated using a cosine equation (see Appendix) derived with sunrise and sunset times for Sheridan, Wyoming (U. S. Nautical Almanac Office 1977). Information is then transferred to second-tier subroutines.

Second Tier Subroutines

Subroutines MALE, FEMALE and JUVENIL compile results for adult males, adult females, and juveniles, respectively. Juvenile energy use is not partitioned by sex because growth rates, hence production costs, are similar in male and female young (Chapter IV); juveniles are non-reproductive (Chapter III) so there are no sex-specific differences in reproductive energy; other sex-specific differences have not been detected. Because adult females reproduce relatively synchronously in Wyoming (Chapter III), the young of a litter period, a cohort, are born together in the model and reach adult body mass at the same time, at approximately 175 days of age (Chapter IV). At 175 days, half of the juveniles are transferred (from JUVENIL) to MALE and half to FEMALE because the sex ratio in collections was 1:1.

FEMALE calls subroutines that compute gestation and lactation energy in addition to other subroutines (Fig. 20). The gestation subroutine (GESTATE) is called at the mean conception dates for the three litters conceived yearly, 6 March, 22 April, and 6 June (Chapter III). The lactation subroutine (LACTATE) is called at mean parturition dates for the litters, 16 April, 2 June, and 17 July. Energy in milk, calculated in LACTATE, is transferred from FEMALE to JUVENIL to support the energy requirements of newborns. The demand of newborns for energy in primary production is zero when they are totally dependent on maternal milk. This period is the first 17 days of lactation in the model. After day 17 of lactation, energy demand not met by milk is taken from the environment (see Tiemeier 1965, Martinet and Demarne 1984).

Third Tier Subroutines

<u>Population</u> <u>Dynamics</u>.--Subroutines JUVSURV and ADSURV compute daily changes in population densities of juveniles and adults, respectively. Mortality rates for black-tailed rather than white-tailed jackrabbits are used because the latter were not available. Since the two species have a large dietary overlap and occupy similar habitat types (Flinders and Hansen 1972), their mortality pressures such as from predators in their habitats are probably similar. Based on a long-term study of black-tailed jackrabbit demography (L. C. Stoddart, unpubl. data), the average mortality rate appears to be slightly higher for juveniles ($0.0062 \cdot km^{-2} \cdot day^{-1}$) than adults ($0.0058 \cdot km^{-2} \cdot day^{-1}$). By 3-4 months of age, 115 days in the model, juvenile and adult mortality rates become equivalent (see Smith 1987).

JUVSURV generates the entry of cohorts of newborn young into the population at the mean parturition date of each litter. Field results from Wyoming (Chapter IV) showed that all adult female jackrabbits were pregnant in the first two litters, and the mean litter sizes were four and six, respectively. In the third litter only 48 percent of females were pregnant with a mean litter size of four. JUVSURV calculates the newborn population per cohort by multiplying together adult female density, pregnancy rate, and mean litter size.

Maintenance and Thermoregulation.--Mass-specific energy requirements per day are computed in the remaining third-tier subroutines. Regression equations in subroutine JUVTHERM model the experimental result that juveniles have a very high maintenance and thermoregulation cost (M + TR) if exposed to moderate to low air temperatures in the first week of life. The cost declines gradually thereafter (Chapter VII). JUVTHERM simulates huddling effects if requested by the user at the program start. Huddling reduces energy use for M + TR linearly, by 35% at T_a = 5 °C to no reduction at T_a = body temperature (Trojan 1969).

Juveniles thermoregulate similarly to adults by 3-4 months of age (Chapter VII), 115 days-old in the model. At 115 days, subroutine JUVENIL calls ADTHERM, the adult thermoregulation subroutine, rather than JUVTHERM. ADTHERM calculates effects of wind on metabolism if windy conditions are inputed by the user. Best fit regression equations for metabolism with or without wind are applied (Chapters VI and VIII). The equations model the energy costs of maintenance and thermoregulation for winter- and summer-acclimatized jackrabbits. Energy use during molt periods is assumed to be intermediate between summer and winter. Wind is not a possible metabolic influence in JUVTHERM. Young animals are smaller than adults and better protected from wind by vegetation and their proximity to the ground.

Specific Dynamic Activity.-- The specific dynamic activity (SDA) is also modeled in JUVTHERM and ADTHERM. Estimated SDA is 27% of basal metabolic rate (BMR), based on results for snowshoe hares (Holter et al. 1974) and other monogastrics (Webster 1983). At present, there is no information on duration of SDA in wild herbivores. Since jackrabbits are active at night (Chapter V), SDA is modeled only for night hours. Infrequent, small feedings, which could occur during the day, produce negligible SDA (Brody 1945). Using the model of Kleiber (1961:274), SDA substitutes for thermoregulatory energy use below the lower critical temperature (LCT) and the fraction substituted for is maximal where BMR + SDA intersects with the slope of metabolic rate on T_a below LCT.

Activity.--The incremental cost of activity is an allometric function of body mass in endotherms (Taylor and Heglund 1982): $kJ \cdot (kg \cdot km)^{-1} = 10.7 \cdot Body\ Mass_{(kg)}^{-0.316}$. Subroutine ACTIVE computes activity energy by inputing body mass (kg) into Taylor and Heglund's equation. The result is multiplied by number of hours of the nighttime activity phase, a function of daylength, and by the average distance (km) moved in 1 hr during the activity phase, which varies seasonally (Chapter V).

Production.--Production subroutines track juvenile and adult body masses and calculate the production energy not due to reproduction. Subroutine JUVPROD computes the growth cost of juveniles by determining their daily gain in body mass from the von Bertalanffy growth curve (Chapter IV). Gain in body mass is converted to energy assuming 3.4 kJ/g (Widdowson 1950). The efficiency of use of metabolizable energy (k) assumed to be 0.70 for juvenile growth (ARC 1980).

Adult production subroutines, ADMPRO and ADFPRO, for males and females, respectively, compute energy costs related primarily to fat deposition and loss. The body mass of adult females increases as they come into breeding condition and decreases post-breeding; the body mass of adult males increases in autumn but decreases in early winter (Chapter IV). These body mass changes are linear in the model. The energy conversion factor employed is 6.3 kJ/g (Gorecki 1965), which is larger than that for juveniles because adults have higher fat contents (Breirem and Homb 1972). Efficiencies of ME utilization for protein and fat are 0.44 and 0.74 in monogastric species, respectively (Breirem and Homb 1972). Since efficiency varies with both level of feeding and metabolizability of food (ARC 1980), an intermediate value, k = 0.60, was used for adult production.

Gestation.--Subroutine GESTATE computes the energy demand during the 42 day gestation period. During each gestation period, body masses of pregnant females increase as fetal and associated tissues accrue. Because data for white-tailed jackrabbits were not available, the fetal growth curve was constructed using data for snowshoe hare (Bookhout 1964). The curve extrapolates to the birth mass of white-tailed jackrabbits and predicts a weight gain of 5 g/day at parturition, which has been reported for the early growth of white-tailed jackrabbits (James and Seabloom 1969b). Fetal growth is similar in jackrabbits and snowshoe hare (Gross et al. 1974, Swihart 1984). GESTATE determines daily gain in fetal mass from the growth curve. The gain is multiplied by mean litter size and by 1.25, to adjust for accessory production (Oftedal 1985). Tissue mass is converted to energy using 3.4 kJ/g (Widdowson 1950). The gestation efficiency, k = 0.40, is based on results of Battaglia and Meschia (1981:110).

Lactation.--Energy of lactation is calculated from the daily milk output of brown hares over a 30 day lactation period (Martinet and Demarne 1984). I converted maternal output of milk per offspring (g) to milk energy (kJ/kg$^{0.75}$) using their data on fat, protein and lactose contents in milk and maternal body mass. Energy conversion factors for milk constituents are reported in Oftedal (1984). A polynomial equation was fit to the milk energy (Y), kJ/kg$^{0.75}$ per lactation day (X): $Y = 44.98 + 8.69\ X - 0.25\ X^2$ ($R^2_a = 0.74$). Because milk energy production by different mammal species is similar if scaled by kg$^{0.75}$ (Lindzell 1972), the equation was used to describe lactation energy in the white-tailed jackrabbit. Subroutine LACTATE finds the value of f(x) from the curve and converts it to mass-specific energy with the maternal body mass of the jackrabbit. The result is then multiplied by litter size and divided by lactation efficiency. Milk output is a direct function of litter size, which holds in litters of up to five or six young (Venge 1963). Lactation efficiency, k, is 0.65 (Close and Fowler 1982, Oftedal 1985).

Expression of Model Output

Energy requirement is expressed as kJ·(kg·day)$^{-1}$ and kJ/day. The former is mass specific. It indicates periods of high energy use per kg of animal tissue. The latter indicates energy requirement per animal. The total energy requirement includes maintenance, thermoregulation, activity, production, and reproduction costs. The thermoregulatory cost is that reduced by substitution by SDA.

Energy demand is expressed as kJ·(km^2·day)$^{-1}$. It takes changes in the density of the jackrabbit population into account. Energy demand comprises all energy animals derive from the environment. Because juvenile energy demand is substituted for by energy in milk (L) during the lactation period, total energy demand = ADM + ADF + JUV - L, where ADM, ADF, and JUV - L are the energy demands of adult males, adult females, and juveniles in the population.

MODEL RESULTS

Energy Requirements

Mass-specific energy costs for maintenance, thermoregulation and activity were similar for adult males and females (Figs. 22, 23). The total maintenance and thermoregulatory requirement reflected the seasonal energetic pattern (Chapter VI): the cost was greater in winter than in summer and intermediate during molt periods. Since basal metabolic rates are 244 and 299 $kJ\cdot(kg\cdot day)^{-1}$ in summer and winter, respectively, the requirement for thermoregulation was minor. Energy use by adult males or females for activity was highest in late winter to early spring. Adult males required most energy at this time.

Positive production, that associated with gain in body mass, requires energy, whereas negative production, the release of stored energy during body mass loss, reduces the energy requirement. In adult males, the production was positive in autumn and negative in early-winter (Fig. 22). Production was positive in pre-breeding and negative in post-breeding females (Fig. 23).

Adult females required most energy per kg during lactation (Fig. 23). The lactation cost was greatest in the second litter, when litter size was largest. Variation in the energy requirement during lactation

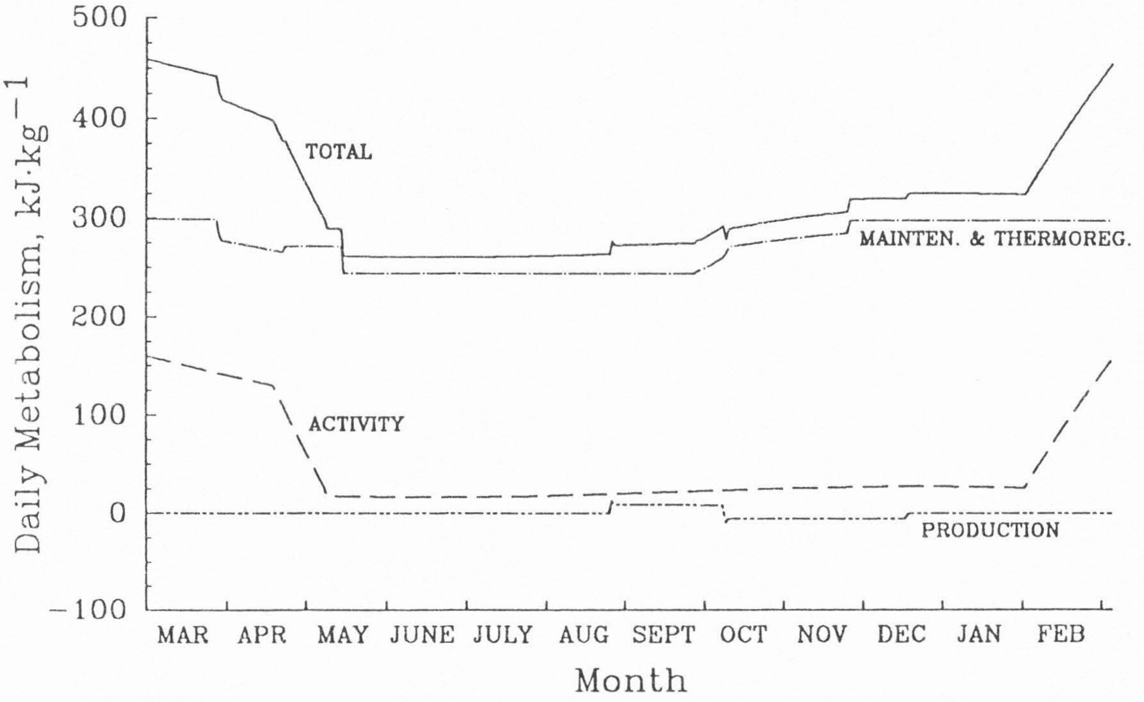

Fig. 22. Estimated mass-specific energy requirements of an adult male jackrabbit.

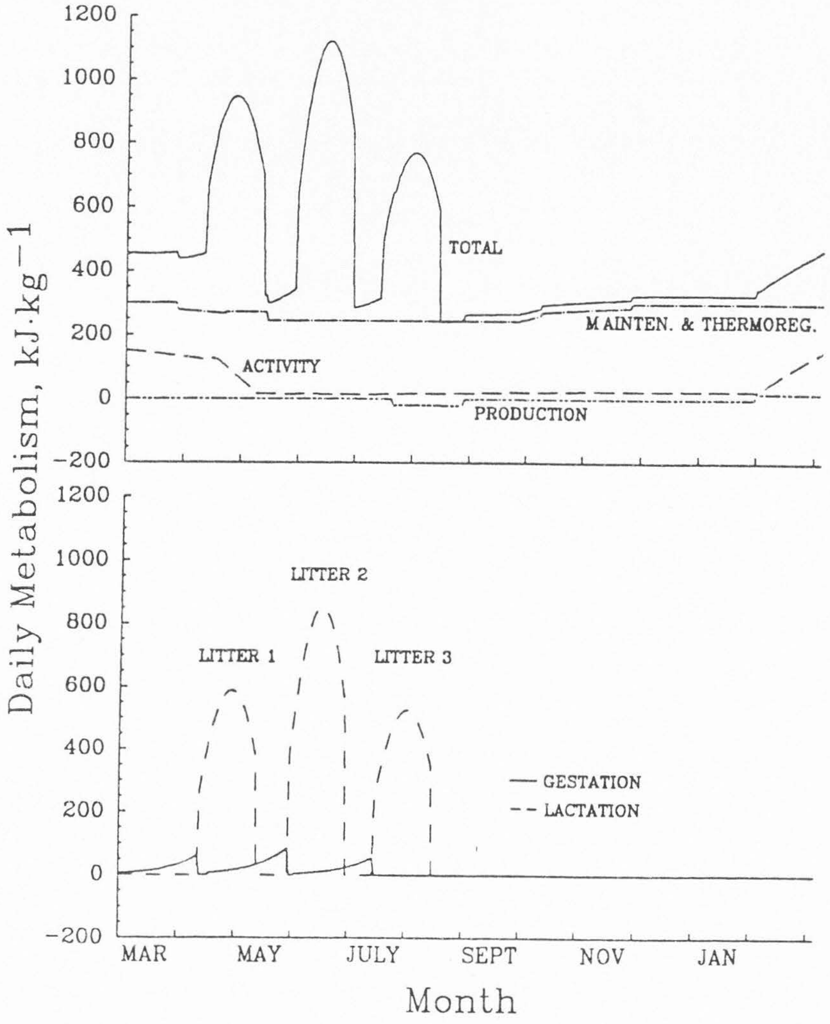

Fig. 23. Estimated mass-specific energy requirements of an adult female jackrabbit.

paralleled changes in milk production. At peak lactation, the energy use was 3 to 5 times maintenance level. The gestation energy was only a fraction of that required for lactation. The cost of gestation increased exponentially and peaked at parturition.

For a juvenile born in any litter period, energy use per kg was extremely high in the first week of life primarily because of a high thermoregulatory energy requirement (Fig. 24). If huddling was simulated, the total requirement in the first week declined by 30, 21 and 19% for litters 1-3, respectively, but energy use remained the highest in newborns. Most energy savings by huddling (30%) occurred in the first litter period because air temperatures were lower than in subsequent litter periods. Juvenile production energy was high initially and declined with age because the body mass gain per kg declined. Juvenile activity cost was negligible.

Adult females required the most energy per animal (Fig. 25). However, outside the breeding season, requirements of adult males and females were similar. Energy use per juvenile born in litter 1, 2 or 3 (L1-L3) was low initially but paralleled energy use of adults by maturation.

Energy Demand

Changes in population density and biomass had a large effect on jackrabbit energy demand on the environment. The population density increased abruptly three times, when cohorts of newborns from three litters were added to the population (Fig. 26). Gradual declines in density occurred because of daily mortality. Biomass changes were due to sigmoidal growth in cohorts of juveniles, body mass gain and loss of

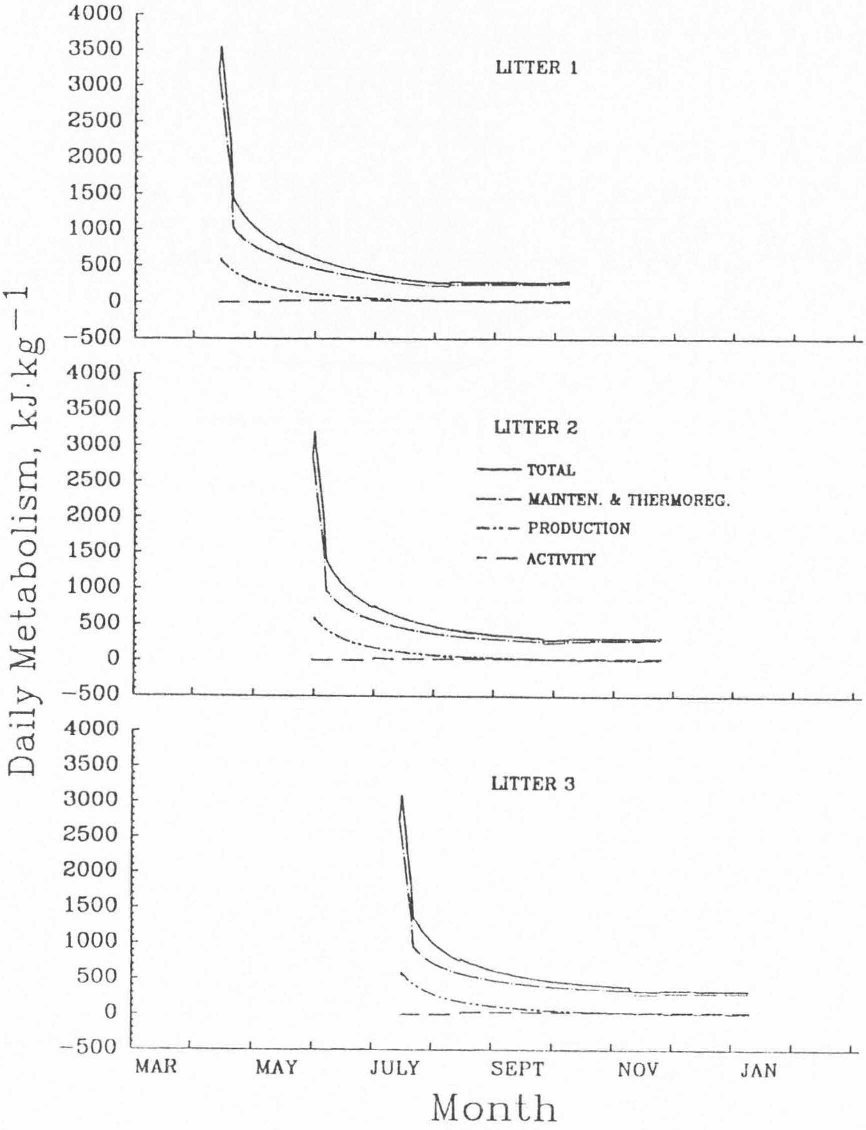

Fig. 24. Estimated mass-specific energy requirements of a juvenile jackrabbit born in litter period 1-3.

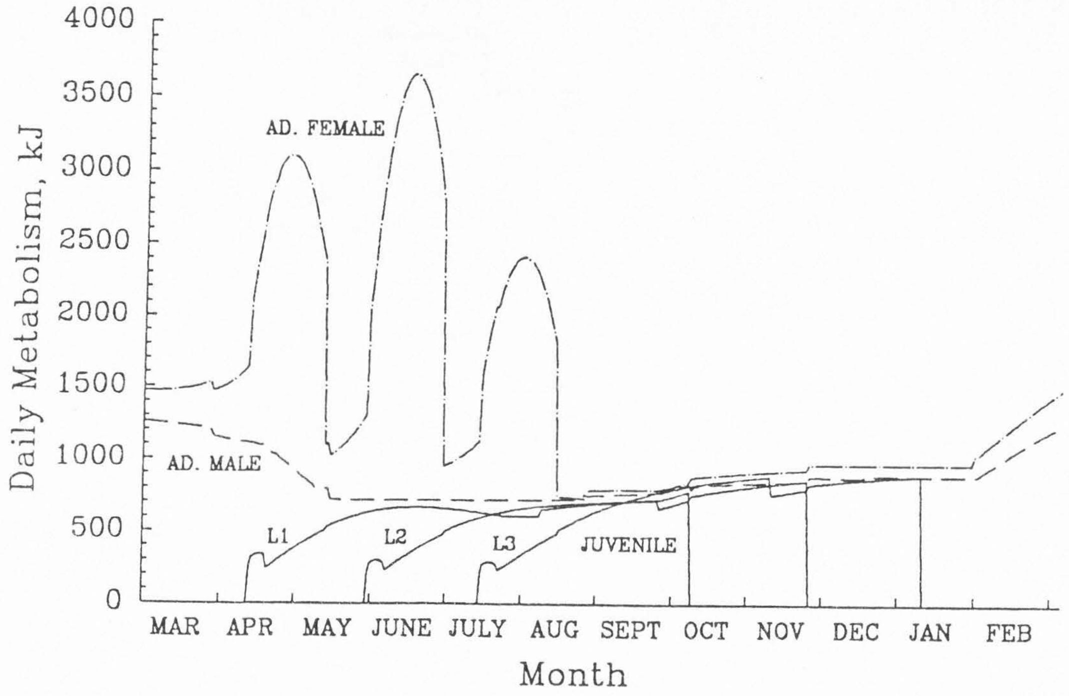

Fig. 25. Estimated energy requirement per animal for an adult male, an adult female, and a juvenile born in litter period 1-3.

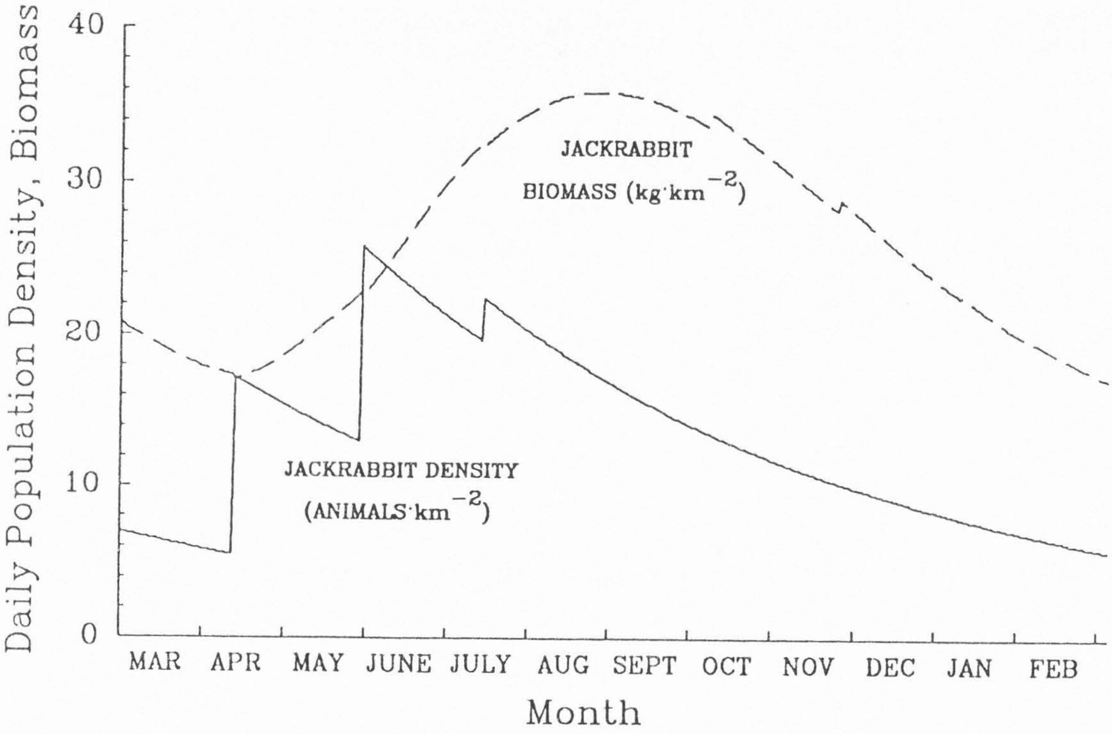

Fig. 26. Simulated changes in population density and biomass, where the pre-breeding population density was 7 jackrabbits/km^2.

adults, and the changes in population density. The population density peaked in June, whereas biomass did not peak until late-summer. The lag between density and biomass peaks reflected chiefly the time required for cohorts to reach asymptotic body mass by sigmoidal growth.

Energy demand was simulated using a pre-breeding population of 7 animals/km^2 (Fig. 27) because this density was found during the field study. Total energy demand was 3820 MJ$\cdot$km$^{-2}\cdot$year^{-1} (the energy cost is 1/7 of this for 1 animal/km^2). Most of the environmental energy demand was from juveniles (41%). Juvenile energy demand increased markedly as cohorts of young were born, and fell markedly as successive cohorts became adults. Adult males and females in the population consumed 24% and 35% of the total energy, respectively. Fluctuations in total energy demand resulted from numerous, cumulative processes. Large, step-wise fluctuations occurred at the onset and cessation of molts in spring (2 April to 18 May) and autumn (10 October to 25 November). These reflected changes in energy use between winter- and summer-acclimatized animals.

Yearly energy demands (MJ$\cdot$individual$^{-1}\cdot$km$^{-2}\cdot$yr^{-1}) for adult males, adult females, juveniles, and all animals were 130, 191, 224 and 546, respectively. Simulated huddling reduced juvenile and total yearly energy demands to 200 (-12%) and 521 (-4%), respectively. Wind increased the total energy demand (Fig. 28). Day and night wind speeds were equivalent in this simulation. Total yearly energy demand (Y) as a function of wind speed (m/s) was: $Y = 549.11 + 56.04 \cdot X - 4.40 \cdot X^2$, $\underline{r} = 0.998$. Changes in energy demand due to air temperature variation at 0.2 m above ground level were analyzed by altering the intercept (curve

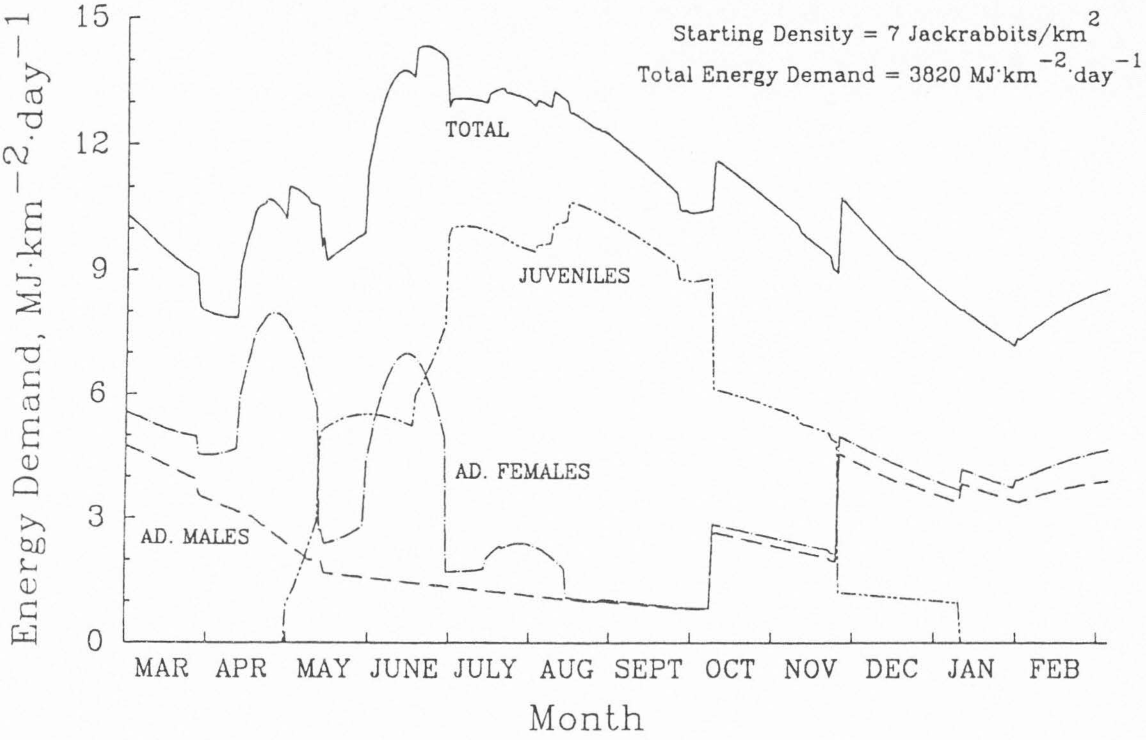

Fig. 27. Estimated energy demand for all adult males, adult females, juveniles in the population, where the pre-breeding population density was 7 jackrabbits/km^2.

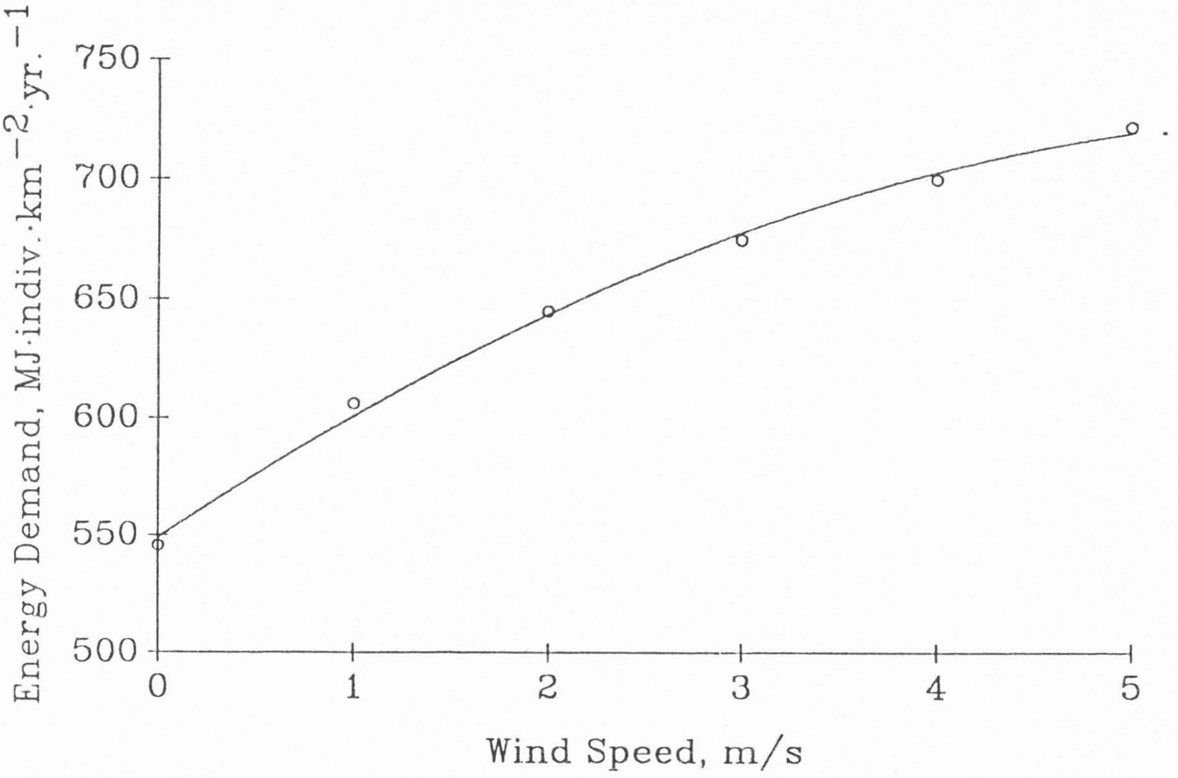

Fig. 28. Simulated effect of wind speed on yearly energy demand.

values were 7.8 °C and 0.5 °C). Daytime and nighttime intercepts were height parameter) of cosine equations (Fig. 21; mean annual intercept varied by the same amount (°C). Very low air temperatures had a large effect on total yearly energy demand but the energy demand was stable at T_a = ±4 °C of the mean annual daytime and nighttime air temperatures (Fig. 29).

DISCUSSION

Energy Use by Jackrabbits

Periods of highest energy cost, potentially constraining periods, differed among the age-sexes classes. Adult females required the most energy during lactation periods. The high energy cost occurred because a mean of four to six young were nursed each litter period and the milk has a high lipid content (Oftedal 1984). The energy requirement of adult males was greatest from late winter to early spring, the onset of the breeding season, because their movement and energy requirement for activity increased. Juveniles required most energy per kg during their first week of life because of their high thermoregulatory energy demand. Although the lowest air temperatures occurred from December to February (Fig. 21), requirements of jackrabbits for energy were not highest in early winter. Only adult animals are in the population during early winter, and their thermoregulatory adaptations to seasonal change in air temperature are well-developed (Chapter VI).

Demand for energy in the environment was related to changes in the density, biomass, and seasonal energy use by population strata. Juveniles born in the three litter periods consumed the most energy per

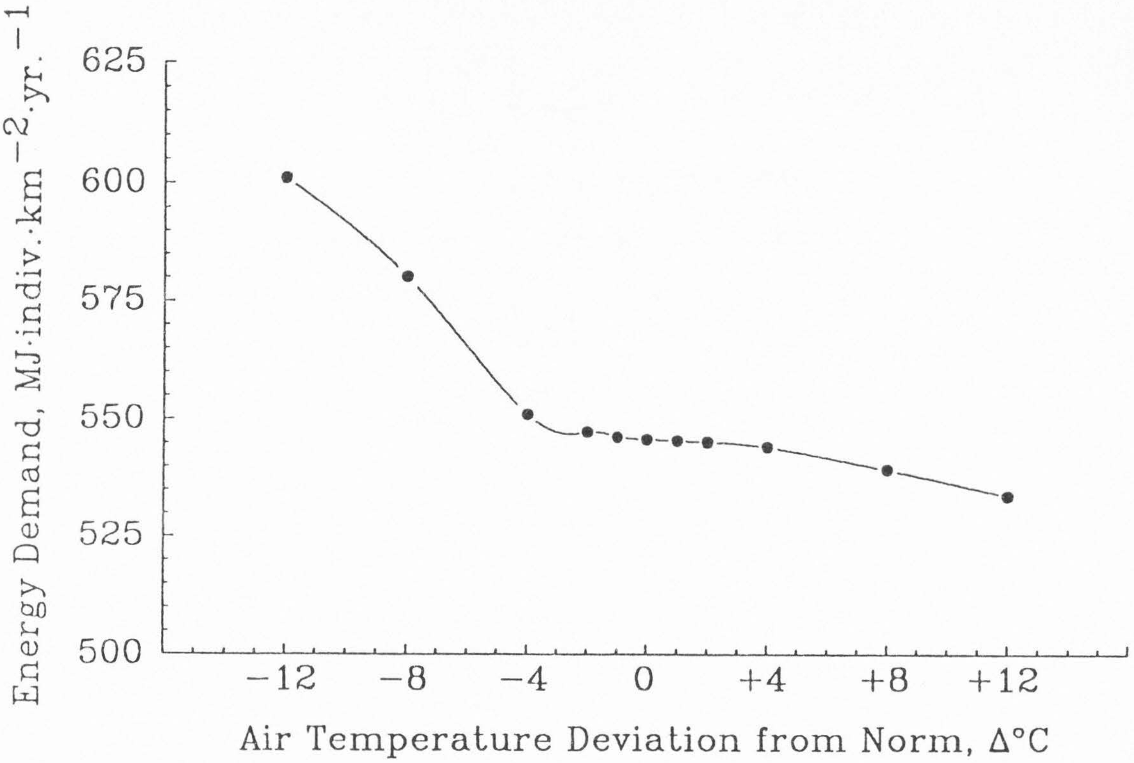

Fig. 29. Simulated effect of a deviation in air temperature from the yearly mean on yearly energy demand.

year. However, when huddling effects were included, adult females consumed almost as much energy (36%) as juveniles (38%). High lactation energy cost elevated the total yearly energy demand of adult females by 47% over adult males. Energy demands of adult females and males were similar outside the breeding season.

Extremely windy conditions elevated the total yearly energy demand markedly (Fig. 28). However, if wind attenuation by vegetation is accounted for, 1 m/s is typical of wind speeds jackrabbits receive during daytime and nighttime hours (Chapter VIII). With a wind speed of 1 m/s, the total yearly energy demands of males, females, juveniles, and all animals increased to 148, 212, 245, and 606 $\mathrm{MJ \cdot individual^{-1} \cdot km^{-2}}$, respectively, which is still 9-14% higher than in calm air. Very low air temperatures increased the total yearly energy cost significantly but the energy demand was relatively constant at air temperatures within 4 °C of the yearly norm in southwestern Wyoming (Fig. 29). Since mean yearly air temperatures seldom deviate more than 1 °C from the yearly norm, yearly energy demand appears stable (between 1985-87, yearly means for daytime and nighttime deviated by <1.2 °C and <0.3 °C, respectively, at 0.2 m above ground level).

Jackrabbit Demand for Energy in Vegetation

The estimated metabolizable energy demand (ME) of jackrabbits was 546 $\mathrm{MJ \cdot individual^{-1} \cdot km^{-2} \cdot yr^{-1}}$ (in calm air). ME is converted to gross energy demand (GE_D) with a metabolizable energy efficiency (ME/GE_D). Efficiencies in natural habitats vary from 0.6 to 0.2. These values represent highly digestible forage and low quality, roughage forage, respectively (0.6 is typical for vegetation in spring; 0.4 for winter and dry season vegetation; 0.2 represents the worst diet available to herbivores because most energy in phytomass cannot be assimilated).

Table 9 shows the estimated standing crop of grasses, forbs, and shrubs on semi-desert areas in Kemmerer, southwestern Wyoming, 1981-87 (N. E. West, unpubl. data). The standing crop was estimated at the growing season end and varied considerably between years. The mean standing crop was 422 $g \cdot m^{-2} \cdot year^{-1}$ (dry matter). Using an energy conversion factor for old-field vegetation, 17.53 kJ/g (Cummins and Wuychek 1971), and adjusting area to km^2, gross energy in the phytomass (GE_P) was $7 \cdot 10^6$ $MJ \cdot km^{-2} \cdot year^{-1}$.

Percent consumption of the standing crop, $GE_D/GE_P \cdot 100$, is obviously affected by changes in jackrabbit population density. The highest recorded density of white-tailed jackrabbits is 32 animals/km^2 (Mohr and Mohr 1936). The amount of forage jackrabbits consume is also affected by phytomass accessibility and palatability (Bryant and Kuropat 1980, Crawley 1983) and metabolizable energy efficiency (MEE). If phytomass palatability, accessibility, or MEE decline, more phytomass energy will be required to fulfill the energy requirement.

The fraction of the standing crop consumed by jackrabbits was estimated using GE_P for Kemmerer, Wyoming and GE_D of white-tailed jackrabbits for southwestern Wyoming (Table 10, top). Estimated consumption by jackrabbits was 0.2% of GE_P at intermediate population densities (10 animals/km^2) with a winter diet (MEE = 0.4). At an unusually high population density, 100 animals/km^2, and the poorest quality forage (MEE = 0.2), only 4% of the phytomass energy was

Table 9. Annual production (g dry matter/m^2) for undisturbed plant communities in Kemmerer, WY (N. E. West, unpubl. data).

Year	Mean	SD
1982	463	412.8
1983	386	281.9
1984	482	406.1
1985	214	209.2
1986	423	338.2
1987	557	434.1

consumed. If the standing crop was only half as large, 8% of the phytomass energy was consumed (assuming 100 jackrabbits/km^2 and MEE = 0.2).

The simulations indicate that the fraction of the total standing crop consumed by the jackrabbit will be small even at very high population densities. At the density of jackrabbits (7 animals/km^2) during the present study, 1985-88, the estimated percent phytomass consumption was only 0.10% of GE_p, assuming an intermediate MEE (0.5). This increased to 0.12% if a wind speed of 1 m/s was applied, decreased to 0.98% if huddling was simulated, and was 0.11% if both wind and huddling were simulated.

Jackrabbits are selective feeders and do not consume all plant parts (Bear and Hansen 1966, Currie and Goodwin 1966). Therefore, I evaluated whether jackrabbit energy demand could exceed forage energy availability by assuming initially that only 50% of vegetation was

Table 10. The effects of varying jackrabbit population density and metabolizable energy efficiency (MEE) on estimated percent use by jackrabbits of phytomass energy in Wyoming semi-desert.

1. All phytomass energy is available.

Animals/km^2 (Spring)	MEE 0.2	MEE 0.4	MEE 0.6
1	0.037	0.018	0.012
10	0.37	0.18	0.12
100	3.7	1.8	1.2

2. 50% of phytomass energy is available.

Animals/km^2 (Spring)	MEE 0.2	MEE 0.4	MEE 0.6
1	0.074	0.037	0.025
10	0.74	0.37	0.25
100	7.4	3.7	2.5

edible (Table 10, bottom). In this case, estimated consumption of forage energy was 0.4% with an intermediate population density (10 animals/km^2) and a winter diet (ME = 0.4). With an unusually high population density (100 animals/km^2) and the lowest quality forage (MEE = 0.2), 7% of the forage energy was consumed. Snow cover during winter might reduce the availability of edible phytomass to as low as 10%. Assuming this extreme condition, 18% of forage energy would be consumed, assuming a winter MEE (0.4) and that the population density remained high (100 animals/km^2).

The scenarios indicate that (1) white-tailed jackrabbits consume only a small fraction of above-ground phytomass energy and (2) white-tailed jackrabbits are not likely to be food limited in the semi-desert area. These conclusions are supported by Anderson and Shumar's (1986) field study. They found that a peak density population of black-tailed jackrabbits could only slightly reduce plant cover. Simulation models also indicate that consumption of forage by black-tailed jackrabbits is negligible (Clark and Innis 1982, Harris 1984).

In contrast, population declines in snowshoe hares could be initiated by food shortage (Keith et al. 1984). Food limitation is more likely when the density of consumers is higher. Snowshoe hares attain higher densities, relative to black-tailed jackrabbits (Fig. 3 in Keith [1983]) or white-tailed jackrabbits (Mohr and Mohr 1936). Several other factors could increase potential food limitation. Snow accumulation could produce a 2-fold decline in the amount of winter browse available to snowshoe hares (Keith 1983). Phytochemicals in vegetation could further limit snowshoe hare populations by reducing forage intake and assimilation (Bryant 1981).

Predation is a contributing factor in snowshoe hare population declines (Keith et al. 1984). Simulations suggest that predator effects alone could account for the population variation in snowshoe hares (Trostel et al. 1987). Predation-related mortality appears to be more important than food limitation in regulating the population density of black-tailed jackrabbits in northern Utah (reviewed by Keith 1983). Mortality (primarily due to predation by coyotes [Canis latrans]) explains much of the variation in numbers of black-tailed jackrabbits (Wagner and Stoddart 1972). The interaction of black-tailed jackrabbits and coyotes may follow a Lotka-Volterra predator-prey oscillation (Wagner and Stoddart 1972, Wagner 1981). Data on predator infuences on white-tailed jackrabbit density are not available. However, population limitation in white-tailed jackrabbits could not be attributed to food limitation because the estimated consumption of edible phytomass was negligible. This suggests that other factors explain population variation in this species.

Applications of the Model

ENERJACK was written to describe the population energy expenditure of white-tailed jackrabbits in a semi-arid, sagebrush-steppe area in southwestern Wyoming (and was derived primarily from data gathered in this region). Use of the model to simulate jackrabbit energy demands in other areas may be inappropriate because energy-requiring processes such as fetal production could differ between regions. For example, more litters are produced during the breeding season in North Dakota (James and Seabloom 1969a) than in Wyoming. However, the model could be modified to describe population energy expenditure in other locations (or in other species). This could be accomplished easily because the algorithms are well-documented (see Appendix).

The model can be used to indicate when animals in a population are most susceptible to disturbance. For example, lactating jackrabbits have a high energy requirement and may be more sensitive to disturbance than other adult females. Newborn jackrabbits have an extremely high energy requirement that may be reduced by huddling. Therefore, a disturbance in huddling activity could have a major effect on energy cost. The model can also be applied to problems in biological control· to predict the life stage of a species that causes most crop damage and when the greatest damage would be expected. For example, juvenile jackrabbits were estimated to consume the most energy in vegetation. Their greatest demand for forage energy was predicted to occur between July and September (Fig. 27). If information on the crop biomass and density of consumers is available, model output can be used to estimate the percent utilization of a crop by consumers (e.g., Table 10, top). Model output can also be used to evaluate the likelihood that a consumer is food limited (e.g., Table 10, bottom).

LITERATURE CITED

Afifi, A. A., and V. Clark. 1984. Computer-aided multivariate analysis. Lifetime Learning Publ., Lond. 458pp.

Alexander, G. 1961. Temperature regulation in the new-born lamb. III. Effect of environmental temperature on metabolic rate, body temperatures, and respiratory quotient. Austr. J. Agric. Res. 12:1152-1174.

-----. 1975. Body temperature control in mammalian young. Br. Med. Bull. 31:62-68.

Anderson, H. L., and P. C. Lent. 1977. Reproduction and growth of the tundra hare (Lepus othus). J. Mamm. 58:53-57.

Anderson, J. E., and M. L. Shumar. 1986. Impacts of black-tailed jackrabbits at peak population densities on sagebrush-steppe vegetation. J. Range Manage. 39:152-156.

Andrews, F., M. Lynch, and E. McGahan. 1978. Rapid metabolic response of the rabbit to a small dose of triiodothyronine (T_3). Irish J. Med. Sci. 147:326-327.

Angerbjörn, A. 1981. Winter food as a limiting factor of dense mountain hare populations on islands. Pages 529-535 in K. Myers and C. D. MacInnes, eds. Proceedings of the world lagomorph conference, August 12-16, 1979. Univ. Guelph, Guelph, Ontario.

Anon. 1984. Solar irradiance assessment for the state of Utah--CY1983, Draft Annu. Rep., Utah AES Project #425. Dep. Soil Sci. Biomet., Utah Agric. Exp. Stn.

ARC. 1980. Requirements for energy. Pages 73-119 in The nutrient requirements of ruminant livestock. Commonwealth Agricultural Bureau, Farnham Royal, England.

Barkworth, M. E., and D. R. Dewey. 1985. Genomically based genera in the perennial Triticeae of North America: Identification and membership. Am. J. Bot. 72:767-776.

Battaglia, F. C., and G. Meschia. 1981. Foetal and placental metabolisms: Their interrelationship and impact upon maternal metabolism. Proc. Nutr. Soc. 40:99-113.

Bayfield, N. G., and R. Hewson. 1975. Automatic monitoring of trail use by mountain hares. J. Wildl. Manage. 39:214-217.

Bear, G. D., and R. M. Hansen. 1966. Food habits, growth and reproduction in white-tailed jackrabbits in southern Colorado. Colo. State Univ., Agr. Exp. Sta., Tech. Bull. 90:1-59.

Bider, J. R. 1961. An ecological study of the hare Lepus americanus. Can J. Zool. 39:81-103.

Bissonnette, T. H., and A. G. Csech. 1939. Modified sexual photoperiodicity in cottontail rabbits. Biol. Bull. 77:364-367.

Blackburn, D. R. 1968. Courtship behavior among white-tailed and black-tailed jackrabbits. Great Basin Nat. 33:203.

Bligh, J., and K. G. Johnson. 1973. Glossary of terms for thermal physiology. J. Appl. Physiol. 35:941-961.

Blix, A. S., and J. B. Steen. 1979. Temperature regulation in newborn polar homeotherms. Physiol. Rev. 59:285-304.

Bookhout, T. A. 1964. Prenatal development of snowshoe hares. J. Wildl. Manage. 28:338-345.

Bradley, S. R., and D. R. Deavers. 1980. A re-examination of the relationship between thermal conductance and body weight in mammals. Comp. Biochem. Physiol. 65A:465-476.

Breirem, K., and T. Homb. 1972. Energy requirements for growth. Pages 547-584 in W. Lenkeit, K. Breirem, and I. Craseman, eds. Handbuch der Tierernährung. Verlag-Paul Parley.

Brody, S. 1945. Bioenergetics and growth. Hafner Publ, N.Y. 1023pp.

Bronson, F. H., and O. W. Tiemeier. 1958. Reproductive and age distribution of black-tailed jackrabbits in Kansas. J. Wildl. Manage. 22:409-414.

Brück, K., and B. Wünnenberg. 1965. Über die Modi der Thermogenese beim neugeborenem Warmblüter. Pflügers Arch. gesamte Physiol. Mensch. Tiere 282:362-375.

Bryant, J. P. 1981. The regulation of snowshoe hare feeding behavior during winter by plant antiherbivore chemistry. Pages 720-731 in K. Myers and C. D. MacInnes, eds. Proceedings of the world lagomorph conference, August 12-16, 1979. Univ. Guelph, Guelph, Ontario.

Bryant, J. P, and P. J. Kuropat. 1980. Selection of winter forage by subarctic browsing vertebrates: The role of plant chemistry. Annu. Rev. Ecol. Syst. 11:261-285.

Burnham, K. P., D. R. Anderson, and J. L. Laake. 1980. Estimation of density from line transect sampling of biological populations. Wildl. Monogr. 72:1-202.

Caceci, M. S., and W. P. Cacheris. 1984. Fitting curves to data. Byte 5:340-362.

Cary, J. R., and L. B. Keith. 1979. Reproductive change in the 10-year cycle of snowshoe hares. Can. J. Zool. 57:375-390.

Cena, K., and J. L. Monteith. 1975. Transfer processes in animal coats. I. Radiative transfer. Proc. R. Soc. Lond. B188:377-393.

Chaffee, R. R. J., and J. C. Roberts. 1971. Temperature acclimation in birds and mammals. Ann. Rev. Physiol. 33:155-202.

Chapman, J. A., A. L. Harman, and D. E. Samuel. 1977. Reproductive and physiological cycles in the cottontail complex in western Maryland and nearby West Virginia. Wildl. Monogr. 56:1-73.

Chappel, R. W., and R. J. Hudson. 1978. Winter bioenergetics of Rocky Mountain bighorn sheep. Can. J. Zool. 56:2388-2393.

Chew, R. M., and A. E. Chew. 1970. Energy relationships of mammals of a desert shrub (*Larrea tridentata*) community. Ecol. Monogr. 40:1-21.

Clark, W. R. 1973. Reproduction, survival and density of snowshoe hares in northeastern Utah. M.S. Thesis, Utah State Univ., Logan. 79pp.

Clark, W. R., and G. S. Innis. 1982. Forage interactions and black-tailed jack rabbit population dynamics: A simulation model. J. Wildl. Manage. 46:1018-1035.

Close, W. H., and V. R. Fowler. 1982. Energy requirements of pigs. Pages 159-174 *in* W. Haresign, ed. Studies in the agricultural and food sciences: Recent advances in animal nutrition. Butterworths, London.

Close, W. H., R. P. Heavens, and D. Brown. 1981. The effects of ambient temperature and air movement on heat loss from the pig. Anim. Prod. 32:75-84.

Conoway, C. H., and H. M. Wight. 1962. Onset of reproductive season and first pregnancy of the season in cottontails. J. Wildl. Manage. 26:278-290.

Cooke, B. D. 1982a. Reduction in food intake and other physiological responses to a restriction of drinking water in captive wild rabbits, Oryctolagus cunniculus (L.). Aust. Wildl. Res. 9:247-252.

-----. 1982b. A shortage of water in natural pastures as a factor limiting a population of rabbits, Oryctolagus cunniculus (L.), in arid, north-eastern South Australia. Aust. Wildl. Res. 9:465-476.

Costa, W. R., K. A. Nagy, and V. H. Shoemaker. 1976. Observations of the behavior of jackrabbits (Lepus californicus) in the Mojave desert. J. Mamm. 57:399-402.

Cowan, D. P., and D. J. Bell. 1986. Leporid social behaviour and social organization. Mammal. Rev. 16:169-179.

Crawley, M. J. 1983. Studies in Ecology. Vol. 10. Herbivory: The dynamics of animal-plant interactions. Blackwell Sci. Publ., U.K. 437pp.

Cummins, K. W., and J. C. Wuychek. 1971. Caloric equivalents for investigations in ecological energetics. Mitt. Intern. Vereing. theor. angew. Limnol. 18:1-158.

Currie, P. O., and D. L. Goodwin. 1966. Consumption of forage by black-tailed jackrabbits on salt desert ranges of Utah. J. Wildl. Manage. 30:304-311.

Davis, G. J, and R. K. Meyer. 1972. The effect of daylength on pituitary FSH and gonadal development of snowshoe hares. Biol. Reprod. 6:264-269.

Dawes, G. S., and G. Mestyán. 1963. Changes in the oxygen consumption of new-born guinea pigs and rabbits on exposure to cold. J. Physiol., Lond. 168:22-42.

Dawkins, M. J. R., and D. Hull. 1964. Brown adipose tissue and the response of new-born rabbits to cold. J. Physiol., Lond. 172: 216-238.

Dawson, T., and K. Schmidt-Nielsen. 1966. Effect of thermal conductance on water economy in the antelope jack rabbit, *Lepus alleni*. J. Cell. Physiol. 67:463-472.

DeJong, A. A. 1976. The influence of simulated solar radiation on the metabolic rate of white-crowned sparrows. Condor 78:174-179.

Donoho, H. S. 1972. Dispersion and dispersal of white-tailed and black-tailed jackrabbits, Pawnee National Grasslands. M.S. Thesis, Colorado State Univ., Fort Collins. 83pp.

Drake, E. 1969. Maintenance and social behavior of captive jack rabbits, *Lepus californicus* Gray. M.S. Thesis, Utah State Univ., Logan. 46pp.

Dumke, R. T. 1973. The white-tailed jackrabbit in Wisconsin. Wis. Dep. Nat. Resour., Final Rep., Pittman-Robertson Study 106, Proj. W-141-R-6. 24pp.

Dunn, J. P., J. A. Chapman, and R. E. Marsh. 1982. Jackrabbits. Pages 124-145 *in* J. A. Chapman and G. A. Feldhammer, eds. Wild mammals of North America. Johns Hopkins Univ. Press, Baltimore.

Farkas, M., I. Várnai, and S. Donhoffer. 1972a. Fallacies in the interpretation of body temperature changes in the newly born. Acta Physiol. Acad. Sci. Hung. 42:31-34.

-----. 1972b. The "correct" frame of reference for comparing metabolic rates: body weight versus body surface. Acta Physiol. Acad. Sci. Hung. 42:35-40.

Feist, D. D., and M. Rosenmann. 1975. Seasonal sympatho-adrenal and metabolic responses to cold in the Alaskan snowshoe hare (Lepus americanus macfarlanii). Comp. Biochem. Physiol. 51A:449-455.

Finch , V. A., R. Dmi'el, R. Boxman, A. Shkolnik, and C. R. Taylor. 1980. Why black goats in hot deserts? Effects of coat color on heat exchanges of wild and domestic goats. Physiol. Zool. 53: 19-25.

Flinders, J. T., and C. L. Elliot. 1979. Abiotic characteristics of black-tailed jackrabbit forms and a hypothesis concerning form function. Encycl. 56:34-38.

Flinders, J. T., and R. M. Hansen. 1972. Diets and habitats of jackrabbits in northeastern Colorado. Colo. State Univ. Range Sci. Dep. Sci. Ser. 12. 29 pp.

-----. 1973. Abundance and dispersion of leporids within a shortgrass ecosystem. J. Mamm. 54:287-291.

Flowerdew, J. R. 1987. Mammals: their reproductive biology and population ecology. Edward Arnold Publ., Lond. 241pp.

Flux, J. E. C. 1970. Life-history of the mountain hare (Lepus timidus scoticus) in north-east Scotland. J. Zool. (Lond.) 161:75-123.

-----. 1971. Validity of the kidney fat index for estimating the condition of hares: a discussion. New Zealand J. Sci. 14:238-244.

-----. 1981. Reproductive strategies in the genus Lepus. Pages 155-174 in K. Myers and C. D. MacInnes, eds. Proceedings of the world lagomorph conference, August 12-16, 1979. Univ. Guelph, Guelph, Ontario.

Fox, J. F., and J. P. Bryant. 1984. Instability of the snowshoe hare and woody plant interaction. Oecologia 63:128-135.

French, N. R., R. McBride, and J. Detmer. 1965. Fertility and population density of the black-tailed jackrabbit. J. Wildl. Manage. 29:14-26.

Garshelis, D. L., H. B. Quigley, C. R. Villarrubia, and M. R. Pelton. 1982. Assessment of telemetric motion sensors for studies of activity. Can J. Zool. 60:1800-1805.

Gates, D. M. 1980. Biophysical ecology. Springer Verlag, N.Y. 611pp.

Gessaman, J. A. 1973. Methods of estimating the energy cost of free existence. Pages 3-31 in J. A. Gessaman, ed. Ecological energetics of homeotherms. Monogr. Ser. Vol. 20, Utah State Univ. Press, Logan.

Gonzales, R. R, M. J. Kluger, and J. D. Hardy. 1971. Partitional calorimetry of the New Zealand white rabbit at temperatures 3-5 °C. J. Appl. Physiol. 31:728-734.

Gorecki, A. 1965. Energy values of body in small mammals. Acta Theriol. 10:333-352.

Gross, J. E., L. C. Stoddart, and F. H. Wagner. 1974. Demographic analysis of a northern Utah jackrabbit population. Wild. Monogr. 40:1-68.

Hall, E. R. 1981. The mammals of North America. Second ed. John Wiley and Sons, N.Y. 600 + 90pp.

Hamilton, J. H. III., and F. Heppner. 1966. Radiant solar energy and the function of black homeotherm pigmentation: An hypothesis. Science 155:196-197.

Harris, G. D. 1984. The winter bioenergetics of Lepus californicus . M.S. Thesis, Utah State Univ., Logan. 101 pp.

Harris, G. D., H. D. Huppi, and J. A. Gessaman. 1985. The thermal conductance of winter and summer pelage of Lepus californicus. J. Thermal Biol. 10:79-81.

Hart, J. S. 1956. Seasonal changes in insulation of the fur. Can. J. Zool. 34:53-57.

-----. 1973. Rodents. Pages 1-149, in G. C. Whittow, ed. Comparative Physiology of Thermoregulation. Vol. 2. Academic Press, N.Y.

Hart, J. S., O. Heroux, W. H. Cottle, and C. A. Mills. 1961. The influence of climate on metabolic and thermal responses of infant caribou. Can. J. Zool. 39:845-856.

Hart, J. S., H. Pohl, and J. S. Tener. 1965. Seasonal acclimatization in varying hare (Lepus americanus). Can. J. Zool. 43:731-744.

Haug, J. C. 1969. Activity and reproduction of the black-tailed jackrabbit in the coastal cordgrass prairie of Texas. M.S. Thesis, Texas A & M Univ., College Station. 116pp.

Hayes, S. R., and J. A. Gessaman. 1980. The combined effects of air temperature, wind and radiation on the resting metabolism of avian raptors. J. Thermal Biol. 5:119-125.

Hayssen, V., and R. C. Lacy. 1985. Basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. Comp. Biochem. Physiol. 81A:741-754.

Heldmaier, G. 1971. Zitterfreie Wärmebildung und Körpergröße bei Säugetieren. Z. vergl. Physiol. 73:222-248.

Heroux, O. 1967. Metabolic adjustments to low temperatures in New Zealand white rabbits. Can. J. Physiol. Pharmacol. 45:451-461.

Hill, R. W. 1972. Determination of oxygen consumption by use of the paramagnetic oxygen analyzer. J. Appl. Physiol. 33:261-263.

Hinds, D. S. 1973. Acclimatization of thermoregulation in the desert cottontail, Sylvilagus auduboni. J. Mamm. 54:708-728.

-----. 1977. Acclimatization of thermoregulation in desert-inhabiting jackrabbits (Lepus alleni and Lepus californicus). Ecology 58: 246-264.

Hofmeyr, M. D. 1985. Thermal properties of the pelages of selected African ungulates. S. Afr. Tydskr. Dierk. 20:179-189.

Holter, J. B., G. Tyler, and T. Walski. 1974. Nutrition of the snowshoe hare (Lepus americanus). Can. J. Zool. 52:1553-1558.

Honda, N., L. D. Carlson, and W. V. Judy. 1963. Skin temperature and blood flow in the rabbit ear. Am J. Physiol. 204:615-618.

Hudson, R. J., and R. G. White. 1985. Computer simulation of energy budgets. Pages 261-290 in R. J. Hudson and R. G. White, eds. Bioenergetics of wild herbivores. CRC Press, Boca Raton.

Hull, D. 1965. Oxygen consumption and body temperature of new-born rabbits and kittens exposed to cold. J. Physiol., Lond. 177: 192-202.

-----. 1973. Thermoregulation in young mammals. Pages 167-200 In G. D. Whittow, ed. Comparative Physiology of thermoregulation. Vol. 3, Academic Press, N.Y.

Hull, D., and M. M. Segall. 1965. The contribution of brown adipose tissue to heat production in the new-born rabbit. J. Physiol., Lond. 181:449-457.

Hutchinson, J. C. D., and G. D. Brown. 1969. Penetrance of cattle coats by radiation. J. Appl. Physiol. 26:454-464.

Irving, L, H. Krog, and M. Monson. 1957. Metabolism of varying hare in winter. Physiol. Zool., 28(3):173-185.

James, T. R., and R. W. Seabloom. 1969a. Reproductive biology of the white-tailed jack rabbit in North Dakota. J. Wildl. Manage. 33: 558-568.

-----. 1969b. Aspects of growth in the white-tailed jack rabbit. Proc. N.D. Acad. Sci. 22:7-14.

Joyce, J. P., and K. L. Blaxter. 1964. The effect of air movement, air temperature and infrared radiation on the energy requirements of sheep. Br. J. Nutr. 18:5-27.

Kanable, A. 1977. Raising rabbits. Rondale, Penn. 191pp.

Keith, L. B. 1964. Daily activity pattern of snowshoe hares. J. Mamm. 45:626-627.

-----. 1981. Population dynamics of hares. Pages 395-440 in K. Myers and C. D. MacInnes, eds. Proceedings of the world lagomorph conference, August 12-16, 1979. Univ. Guelph, Guelph, Ontario.

-----. 1983. Role of food in hare population cycles. Oikos 40:385-395.

Keith, L. B., J. R. Cary, O. J. Rongstad, and M. C. Brittingham. 1984. Demography and ecology of a declining snowshoe hare population. Wildl. Monogr. 90:1-43.

Keith, L. B., and L. A. Windberg. 1978. A demographic analysis of the snowshoe hare cycle. Wildl. Monogr. 58:1-70.

Kleiber, M. 1961. The fire of life, an introduction to animal energetics. John Wiley and Sons, N.Y. 454pp.

Kline. P. D. 1963. Notes on the biology of the jackrabbit in Iowa. Ia. Acad. Sci. 70:196-204.

Knowlton, F. F., P. E. Martin, and J. C. Haug. 1968. A telemetric monitor for determining animal activity. J. Wildl. Manage. 32: 943-948.

Kokova, J., and L. Jansky. 1968. Cold acclimation in the rabbit. Physiol. Bohem. 17:309-316.

Kolodeznikova, E. D., and J. I. Afanasiev. 1980. Brown fat reaction to extreme exposures. Adv. Physiol. Sci. 32:519-521.

Kruk, B., J. Lyszczarz, E. Boruta, and R. Grucza. 1981. Effect of prolonged exposure to heat on the thermoregulatory reactions to high ambient temperatures in rabbits. Acta Physiol. Pol. 32: 219-221.

Kuvlevsky, W. P., and L. B. Keith. 1983. Demography of snowshoe hare populations in Wisconsin. J. Mamm. 64:233-244.

Lechleitener, R. R. 1958. Certain aspects of behavior of the black-tailed jackrabbit. Am. Midl. Nat. 60:145-155.

-----. 1959. Sex ratio, age classes and reproduction of the black-tailed jack rabbit. J. Mamm. 40:63-81.

Lemnell, P. A. and B. Lindlöf. 1981. Diurnal and seasonal activity pattern in the mountain hare. Pages 349-356 in K. Myers and C. D. MacInnes, eds. Proceedings of the world lagomorph conference, August 12-16, 1979. Univ. Guelph, Guelph, Ontario.

Lentz, C. P., and J. S. Hart. 1960. The effect of wind and moisture on heat loss through the fur of newborn caribou. Can. J. Zool. 38:679-688.

Levins, R. 1966. The strategy of model building in population biology. Am. Sci. 54:421-431.

Lincoln, R. J., G. A. Boxshall, and P. F. Clark. 1982. A dictionary of ecology, evolution and systematics. Cambridge Univ. Press, U.K. 298pp.

Lindlöf, B. 1978. Aggressive dominance rank in relation to feeding by European hare. Viltrevy 10:145-158.

Lindlöf, B., E. Lindström, and A. Pehrson. 1974. On activity, habitat selection and diet of the mountain hare (Lepus timidus L.) in winter. Viltrevy 9:27-41.

Lindzell, J. L. 1972. Milk yield, energy loss in milk, and mammary gland weight in different species. Dairy Sci. Abstr. 34:351-360.

Lockard, R. B., and D. H. Owings. 1974. Moon-related surface activity of bannertail (Dipodomys spectabilis) and Fresno (D. nitratoides) kangaroo rats. Anim. Behav. 22:262-273.

Lustick, S. 1969. Bird energetics: effects of artificial radiation. Science 163:387-389.

Lyman, C. P. 1943. Control of coat color in the varying hare Lepus americanus Erxleben. Bull. Mus. Comp. Zool. 93:393-461.

Martinet, L., and Y. Demarne. 1984. Nursing behaviour and lactation in the brown hare (*Lepus europaeus*) raised in captivity. Acta Zool. Fenn. 171:187-190.

Matuszewski, G. 1981. Circadian activity of european hares in spring, on the Kampinos Forest border. Pages 357-365 *in* K. Myers and C. D. MacInnes, eds. Proceedings of the world lagomorph conference, August 12-16, 1979. Univ. Guelph, Guelph, Ontario.

McClure, P. A., and W. P. Porter. 1983. Development of insulation in neonatal cotton rats (*Sigmodon hispidus*). Physiol. Zool. 56:18-32.

McNab, B. K. 1970. Body weight and the energetics of temperature regulation. J. Exper. Biol. 53:329-348.

-----. 1980. On estimating thermal conductance in endotherms. Physiol. Zool. 53:145-156.

Mech, L. D., K. L. Heezeen, and D. B. Siniff. 1966. Onset and of activity in cottontail rabbits and snowshoe hares in relation to sunset and sunrise. Anim. Behav. 14:410-413.

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

Millar, J. S. 1981. Pre-partum reproductive characteristics of eutherian mammals. Evolution 35:1149-1163.

Mohr, W. P., and C. O. Mohr. 1936. Recent jack rabbit populations at Rapidan, Minnesota. J. Mamm. 17:112-114.

Moote, I. 1955. The thermal insulation of caribou pelts. Text. Res. J. 25:832-837.

Morrison, D. W. 1978. Lunar phobia in a neotropical fruit bat, Artibeus jamaicensis (Chiroptera: Phyllostomidae). Anim. Behav. 26:852-855.

Myers, K., and W. E. Poole. 1962. A study of the biology of the wild rabbit, Oryctolagus cunniculus (L.) in confined populations. III. Reproduction. Aust. J. Zool. 10:225-267.

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

Neal, C. M. 1976. Energy budget of the chipmunk (Tamias striatus): convective heat loss. Comp. Biochem. Physiol. 54:157-160.

Neal, C. M., and S. I. Lustick. 1975. Energy budget of the eastern chipmunk (Tamias striatus): artificial radiation. Comp. Biochem. Physiol. 50A:233-236.

Newson, J. 1964. Reproduction and prenatal mortality of snowshoe hares on Manitoulin Island, Ontario. Can. J. Zool. 42:987-1005.

NOAA. 1985-87. Climatological data, Wyoming. Environ. Data Inf. Serv., Natl. Climatic Data Cent., Asheville, N.C.

Oftedal, O. T. 1984. Milk composition, milk yield and energy output at peak lactation: A comparative review. Symp. Zool. Soc. Lond. 51:33-85.

-----. 1985. Pregnancy and lactation. Pages 215-238 in R. J. Hudson and R. G. White, eds. Bioenergetics of wild herbivores. CRC Press, Boca Raton, Fla.

Pease, J. L., R. H. Vowles, and L. B. Keith. 1979. Interaction of snowshoe hares and woody vegetation. J. Wildl. Manage. 43:43-60.

Porter, W. P. 1969. Thermal radiation in metabolic chambers. Science 166:115-117.

Ralls, K. 1976. Mammals in which females are larger than males. Q. Rev. Biol. 51:245-276.

Richards, G. C. 1979. Variation in water turnover by wild rabbits, _Oryctolagus cunniculus_, in arid environment due to season, age group and reproductive condition. Aust. Wildl. Res. 6:289-296.

Robbins, C. T. 1983. Wildlife feeding and nutrition. Academic Press, N.Y. 343pp.

Rogowitz, G. L. 1988. Measurement of simultaneous effects of air temperature, wind speed and short-wave irradiance on animal metabolism: a wind tunnel design. J. Physics E: Sci. Instrum. 21:903-904.

Ryszkowski, L. and N. R. French. 1982. Trophic impact of mammals in terrestrial ecosystems. Acta Theriol. 27:3-24.

Sadleir, R. M. F. S. 1969. The ecology of reproduction in wild and domestic mammals. Methuen, Lond. 321pp.

Sadleir, R. M. F. S. 1972. Environmental effects. Pages 69-93 _in_ C. R. Austin and R. V. Short, eds. Reproduction in Mammals. Book 4: Reproductive Patterns. University Press, Cambridge.

Schmidt-Nielsen, K., T. J. Dawson, H. T. Hammel, and D. C. Jackson. 1965. The jackrabbit: a study in its desert survival. Hvalradets Skr. 48:125-142.

Scholander, P. F., V. Walters, R. Hock, and L. Irving. 1950. Body insulation of some arctic and tropical mammals and birds. Biol. Bull. 99:225-236.

Schwartz, C. 1973. The cottontail and white-tailed jackrabbit in Iowa, 1963-1972. Ia. Wildl. Res. Bull. 6:1-23.

Scopes, J. W., and J. P. M. Tizard. 1963. The effect of intravenous noradrenaline on the oxygen consumption of new-born mammals. J. Physiol. 165:305-326.

Severaid, J. H. 1942. The snowshoe hare: its life history and artificial propagation. Maine Dep. Inland Fish. Game, Augusta. 95 pp.

Shoemaker, V. H., K. A. Nagy, and W. R. Costa. 1976. Energy utilization and temperature regulation by jackrabbits (Lepus californicus) in the Mojave Desert. Physiol. Zool. 49:364-375.

Smith, G. W. 1987. Mortality and movement within a black-tailed jackrabbit population. Ph.D. Thesis, Utah State Univ., Logan. 101pp.

Smith, G. W., and N. C. Nydegger. 1985. A spotlight line-transect method for surveying jack rabbits. J. Wildl. Manage. 49:699-702.

Stodart, E., and K. Myers. 1966. The effects of different foods on confined populations of wild rabbits, Oryctolagus cunniculus (L.). CSIRO Wild. Res. 11:111-124.

Stoddart, L. C. 1985. Severe weather related mortality of black-tailed jack rabbits. J. Wildl. Manage. 49:696-698.

Swihart, R. K. 1984. Body size, breeding season length, and life history tactics of lagomorphs. Oikos 43:282-290.

Taylor, C. R., and N. C. Heglund. 1982. Energetics and mechanics of partial correlation coefficients showed that SEASON explained the most terrestrial locomotion. Annu. Rev. Physiol. 44:97-107.]

Tiemeier, O. W. 1965. The black-tailed jackrabbit in Kansas: I. Bionomics. Kans. State Univ. Agric. Exper. Sta. Tech. Bull. 140. 75pp.

Tomasi, T. E, and B. A. Horwitz. 1987. Thyroid function and cold acclimation in the hamster, Mesocricetus auratus. Am. J. Physiol. 252E:260-267.

Tregear, R. T. 1965. Hair density, wind speed, and heat loss in mammals. J. Appl. Physiol. 20:796-801.

Trojan, P. 1969. An ecological model of the costs of maintenance of Microtus arvalis (Pall.). Pages 113-122 in K. Petrusewicz and L. Ryszkowski, eds. Energy flow through small mammal populations, Warszawa. Proc. IBP meeting on secondary productivity in small mammal populations, Oxford, England, July 29th-August 2nd, 1978.

Trostel, K., A. R. E. Smith, and C. J. Krebs. 1987. Can predation cause the 10-year hare cycle? Oecologia 74:185-192.

U.S. Nautical Alamanac Office. 1977. Sunrise and sunset tables for key cities and weather stations of the U.S. Gale Research, Detroit. 350pp.

U.S. Naval Observatory. 1946. Tables of sunrise, sunset, and twilight, supplement to the American ephemeris. U.S. Gov. Print. Off., Washington, D.C.

Vaughan, M., and L. B. Keith. 1981. Demographic response of experimental snowshoe hare populations to overwinter food shortage. J. Wildl. Manage. 45:354-380.

Venge, O. 1963. The influence of nursing behaviour and milk production on early growth in rabbits. Anim. Behav. 4:500-506.

Wagner, F. H. 1981. Role of lagomorphs in ecosystems. Pages 668-694 in K. Myers and C. D. MacInnes, eds. Proceedings of the world lagomorph conference, August 12-16, 1979. Univ. Guelph, Guelph, Ontario.

Wagner, F. H., and L. C. Stoddart. 1972. Influence of coyote predation on black-tailed jackrabbit populations in Utah. J. Wildl. Manage. 36:329-342.

Walsberg, G. E., G. S. Campbell, and J. R. King. 1978. Animal coat color and radiative heat gain: A re-evaluation. J. Comp. Physiol. 126:211-222.

Wang, L. C. H., D. L. Jones, R. A. MacArthur and W. A. Fuller. 1973. Adaptation to cold: energy metabolism in an atypical lagomorph, the arctic hare (Lepus arcticus). Can. J. Zool. 51:841-846.

Webster, A. J. F. 1974. Adaptation to cold. Pages 71-106 in D. Robershaw, ed. MTP Intern. Rev. Sci., Physiol Ser. 1., Vol. 7: Environmental physiology. Butterworths, Lond.

Webster, A. J. F. 1983. Energetics of maintenance and growth. Pages 178-207 in L. Girardier and M. J. Stock, eds. Mammalian thermogenesis. Chapman and Hall, N.Y.

West, N. E. 1983. Western intermountain sagebrush steppe. Pages 351-374 in N. E. West, ed. Temperate deserts and semi-deserts. Elsevier Press, Amsterdam.

Widdowson, E. M. 1950. Chemical composition of newly born mammals. Nature 14:626-628.

-----. 1981. The role of nutrition in mammalian reproduction. Pages 145-159 *in* D. Gilmore and B. Cook, eds. Environmental factors in mammalian reproduction. University Park Press, Baltimore.

Wolton, R. J. 1983. The activity of free-ranging wood mice *Apodemus sylvilaticus*. J. Anim. Ecol. 52:781-794.

Zullinger, E. M., R. E. Ricklefs, K. H. Redford, and G. M. Mace. 1984. Fitting sigmoidal equations to mammalian growth data. J. Mamm. 65:607-637.

APPENDIX

APPENDIX: PROGRAM ENERJACK

(FORTRAN CODE)

```
C*******************************************************************
C*******************************************************************
C*******************************************************************
C**************** P R O G R A M   E N E R J A C K ***************
C*******************************************************************
C*******************************************************************
C*******************************************************************
C
C                     PROGRAM ENERJACK
C              TO MODEL JACKRABBIT ENERGETICS
C
C
C*******************************************************************
C****************** Y E A R L Y   C L O C K ********************
C*******************************************************************
          REAL D,DAY,DAYLEN,TEMP(2),WIND(2),POPINIT
          REAL ADMPOP,ADFPOP,JPOP
          REAL MMASS,FMASS,JMASS,ADMENER,ADFENER,JENER
          REAL NEWPOP,JUVPOP(3),ADMMASS,ADFMASS
          REAL AVGTEMP,AVGWIND,TOTMASS,TOTPOP,TOTENER,YEAREN
          REAL OLDMMASS,OLDFMASS
          REAL MALEKJ,FEMKJ,JUVKJ(3),MALETOT,FEMTOT,JUVTOT
          INTEGER MFLAG,FFLAG,JFLAG,HUDFLAG
          COMMON /DAYS/ DAY,DAYLEN
          COMMON /STEP/ D
          COMMON /ENVIRON/ TEMP,WIND
          COMMON /JUV/ JUVKJ,JUVPOP,NEWPOP,ADFPOP,JFLAG
          COMMON /ADM/ MALEKJ,MFLAG,ADMMASS
          COMMON /ADF/ FEMKJ,FFLAG,ADFMASS
          COMMON /M/ OLDMMASS
          COMMON /F/ OLDFMASS
          COMMON / MANIP / HUDFLAG
       OPEN(UNIT=6,FILE='ENERJACK.OUT',STATUS='NEW',RECL=200)
       OPEN(UNIT=7,FILE='ADMIND.OUT',STATUS='NEW',RECL=200)
       OPEN(UNIT=8,FILE='ADFIND.OUT',STATUS='NEW',RECL=200)
       OPEN(UNIT=1,FILE='JUVIND1.OUT',STATUS='NEW')
       OPEN(UNIT=2,FILE='JUVIND2.OUT',STATUS='NEW')
       OPEN(UNIT=3,FILE='JUVIND3.OUT',STATUS='NEW')
       OPEN(UNIT=4,FILE='ALLKJ.OUT',STATUS='NEW')
C------------------------------------------------------------
C THIS IS THE MAIN PROGRAM FOR ENERJACK:  THE YEARLY CLOCK
C
C NOTE THAT THE FOLLOWING COMMENTS ARE NUMBERED TO CORRESPOND TO
C SECTIONS IN THE PROGRAM THAT FOLLOW.
C
C THE MAIN PROGRAM (YEARLY CLOCK) HAS THE FOLLOWING FUNCTIONS:
```

```
C        1. INITIALIZATION
C
C        1.A. IT 1ST ASKS IF YOU REQUEST A DETAILED PRINTOUT FOR THE
C           DIFFERENT MODEL SUBCOMPONENTS.  THIS IS A
C           BREAKDOWN OF ENERGY (KJ/INDIVIDUAL/DAY) AND HOW ENERGY
C           IS PARTITIONED (SEE MALE, FEMALE AND JUVENILE CLOCKS).
C           (SEE ALSO NOTE AT END OF THESE COMMENTS)
C
C             USER THEN INPUTS MEAN DAYTIME AND MEAN NIGHTTIME
C                WIND SPEED (M/S) FOR USE IN SIMULATION
C             YOU ARE ASKED IF YOU WISH TO SIMULATE HUDDLING
C             BASED ON A LINEAR REDUCTION IN JUVENILE METABOLIC
C             RATE (MR).  This is a 0% reduction at Ta = 39C to
c          a 40% reduction at OC, based on work of Trojan (1969).
C
C        1.B  THE INITIAL POPULATION DENSITY (POPINIT) IS ENTERED
C
C        1.C TOTAL ENERGY COSTS (kJ/KM^2*YEAR) ARE SET TO 0
C
C        2. THE MODEL USES THE INITIAL POPULATION DENSITY (POPINIT)
C            TO COMPUTE MALE AND FEMALE POPULATION DENSITY, WHERE
C                50% ARE FEMALE, 50% ARE MALE (1:1 SEX RATIO ASSUMED)
C            A LOOP IS BEGUN WHICH INCREMENTS FOR THE MODEL TIME STEP.
C            THE LOOP RUNS 365 DAYS AND BEGINS ON DAY=65 (THE ONSET
C             OF THE BREEDING SEASON).  TIME STEP IS ONE DAY.
C
C        3.  VALUES FOR THESE VARIABLES ARE CALCULATED:
C
C        D       = TIME STEP OF MODEL (1 TO 365 BY 1)
C        DAY     = DAY OF YEAR (65 TO 365, THEN 1 TO 64)
C                        note that DAY 1 = JANUARY 1st
C        DAYLEN  = DAYLENGTH (IN HOURS) - A COSINE FUNCTION DEVELOPED
C                  FROM SUNRISE & SUNSET TIMES AT SHERIDAN, WYOMING.
C        TEMP(P) = AIR TEMPERATURE (C) IN SW WYOMING (GROUND LEVEL) FOR
C                  DAYS (P = 1) AND NIGHTS (P=2) -TWO COSINE FUNCTIONS
C        AVGTEMP = AVERAGE DAILY TEMPERATURE (C) FOR 24 HR PERIOD
C        AVGWIND = AVERAGE DAILY WIND SPEED (M/S) FOR 24 HR. PERIOD
C
C        4. THE YEARLY CLOCK THEN DIRECTS INPUT TO AND
C           COLLECTS OUTPUT FROM 3 SUBROUTINES (REFER TO THEM FOR
C           MORE DETAILED INFORMATION). THE SUBROUTINES ARE:
C
C             4A. THE ADULT MALE CLOCK    = SUBROUTINE MALE
C                 VARIABLE NAMES:
C                        ADMPOP = POPULATION DENSITY (PER KM^2*DAY)
C                        MMASS = POPULATION BIOMASS (KG/DAY)
C                        ADMENER = POPULATION ENERGY (KJ/KM^2*DAY)
C
C             4B. THE ADULT FEMALE CLOCK = SUBROUTINE FEMALE
C                 VARIABLE NAMES ARE SIMILAR:
C                        ADFPOP, FMASS, ADFENER
C                               (UNITS AS ABOVE)
```

```
C
C            4C. THE JUVENILE CLOCK   = SUBROUTINE JUVENIL
C                VARIABLE NAMES ARE SIMILAR:
C                       JPOP, JMASS, JENER
C                               (UNITS AS ABOVE)
C
C. 4D.   VALUES ARE SUMMED FROM THE SUBROUTINES (ENERGY UNIT IS
C          kJ/KG*DAY).
C
C        WHEN JUVENILES BECOME ADULTS (see SUBROUTINE JUVENIL), NEW
C        POPULATION (newpop) IS ADDED TO POPULATIONS OF ADULT MALES
C        AND FEMALES (1:1 SEX RATIO).
C
C                        *******************
C. 5.        INFORMATION FROM 4A-4D ABOVE IS THEN PRINTED
C                        *******************
C          FILE "ENERJACK.OUT" CONTAINS ENERGY OUTPUT THAT TAKES
C          CHANGE IN POPULATION DENSITY INTO ACCOUNT. THEREFORE,
C               ENERGY IS EXPRESSED IN TERMS OF KJ/KM^2*DAY.
C        Energy use is in terms of demand on environment.
c
C              ORDER OF ITEMS IN FILE FROM LEFT TO RIGHT:
C
C        D       = LINE NUMBER (1-365)
C        DAY     = DAY OF YEAR (65-365 AND THEN 1-64)
C        AVGTEMP = MEAN DAILY TEMPERATURE (CELSIUS)
C        AVGWIND = MEAN DAILY WIND (METER/SEC)
C        TOTPOP  = POPULATION DENSITY (INDIVID./*KM^2*DAY)
C        TOTMASS = POPULATION BIOMASS (Kg/KM^2*DAY)
C        TOTENER = POPULATION ENERGY DEMAND (kJ/KM^2*DAY)
C        ADMENER = ENERGY DEMAND OF ALL MALES IN POPUL. (kJ/KM^2*DAY)
C        ADFENER = ENERGY DEMAND OF ALL FEMALES IN POPUL. (kJ/KM^2*DAY)
C        JENER   = ENERGY DEMAND OF ALL JUVENIL. IN POPUL. (kJ/KM^2/DAY)
C
C                       *********************
C
C        FILE "ALLKJ.OUT" CONTAINS INFORMATION ON ABSOLUTE ENERGY
C        REQUIREMENT (UNITS ARE kJ/DAY).  REQUIREMENT IS independent of
C        change in population density.
c
c                     OUTPUT IN FILE FROM LEFT TO RIGHT:
C
C        D       = LINE NUMBER
C        DAY     = DAY OF YEAR
C        MALEKJ  = ENERGY USE OF ONE MALE (kJ/DAY)
C        FEMKJ   = ENERGY USE OF ONE FEMALE (kJ/DAY)
C        JUVKJ(1) = ENERGY USE OF ONE 1ST LITTER JUVENILE (kJ/DAY)
C        JUVKJ(2) = ENERGY USE OF ONE 2ND LITTER JUVENILE (kJ/DAY)
C        JUVKJ(3) = ENERGY USE OF ONE 3RD LITTER JUVENILE (kJ/DAY)
C
C                       ************************
C
```

```
C       NOTE: IF REQUESTED BY USER AT PROGRAM START, ADDITIONAL
C       FILES ARE PRINTED. FOR ENERGY IN UNITS OF kJ/KG*DAY WHICH IS
C       independent of population density, REFER TO OUTPUT PRINTED
C               --> IN SUBROUTINE MALE (file "ADMIND.OUT")
C               --> IN SUBROUTINE FEMALE (file "ADFIND.OUT")
C               --> IN SUBROUTINE JUVENIL (in three files :
C                       "JUVIND1.OUT","JUVIND2.OUT", "JUVIND3.OUT"
C                       for litter 1, 2 and 3, respectively
C
C    TOTAL ENERGY REQUIREMENT AND ENERGY REQUIREMENT FOR MAINTENANCE +
C               THERMOREGULATION, PRODUCTION, ACTIVITY,
C               GESTATION AND LACTATION ARE REPORTED.
C
C                       *************************
C
C. 6.         ENERGY TOTALS ARE PRINTED TO SCREEN AT END OF RUN:
C
C               YEAREN = TOTAL POPULATION ENERGY (kJ/KM^2*YEAR)
C               MALETOT = TOTAL ADULT MALE ENERGY (kJ/KM^2*YEAR)
C               FEMTOT = TOTAL ADULT FEMALE ENERGY (kJ/KM^2*YEAR)
C               JUVTOT = TOTAL JUVENILE ENERGY (kJ/KM^2*YEAR)
C------------------------------------------------------------------
C.1A.
        PRINT*,'TYPE "1" TO PRINT OUT, OR "0" TO OMIT PRINTING:'
        PRINT*,'             FOR THE FOLLOWING:'
        PRINT*,' '
        PRINT*,'PRINT ALL RESULTS FOR JUVENILES, ENTER "1" OR "0"'
        READ*,JFLAG
        PRINT*,' '
        PRINT*,'PRINT ALL RESULTS FOR ADULT FEMALES, ENTER "1" OR "0"'

        READ*,FFLAG
        PRINT*,' '
        PRINT*,'PRINT ALL RESULTS FOR ADULT MALES, ENTER "1" OR "0"'
        READ*,MFLAG
        PRINT*,' '
          PRINT*,'INPUT DAYTIME WIND SPEED --->'
          READ*, WIND (1)
          PRINT*,' '
          PRINT*,'INPUT NIGHTTIME WIND SPEED --->'
          READ*,WIND (2)
          PRINT*,' '
          PRINT*,'ENTER "0" FOR NO HUDDLING SIMULATION"'
          PRINT*,'   OR "1" TO SIMULATE HUDDLING."'
          READ*,HUDFLAG
          PRINT*,' '
C.1B.
        PRINT*,'INPUT INITIAL POPULATION DENSITY OF ADULTS---->'
        READ*,POPINIT
C.1C.
         YEAREN = 0.0
         MALETOT = 0.0
```

```
            FEMTOT  = 0.0
            JUVTOT  = 0.0
C.2
           ADFPOP = 0.5*POPINIT
           ADMPOP = ADFPOP
          DO D = 1,365
             IF (D.LE.301.0)THEN
               DAY = D + 64.0
             ELSE
               DAY= D - 301.0
             END IF
C.3
            DAYLEN = 12.22 + 3.38*COS(0.0172*(DAY - 172.0))
            TEMP(1) = 7.77+13.73*COS(0.0172*(DAY-194.3))
            TEMP(2) = 0.51+10.96*COS(0.0172*(DAY-197.8))
            AVGTEMP=(TEMP(1)*DAYLEN/24.0)+(TEMP(2)*(24.0-DAYLEN)/24.0)
            AVGWIND=(WIND(1)*DAYLEN/24.0)+(WIND(2)*(24.0-DAYLEN)/24.0)
C.4A
              CALL MALE (ADMPOP,MMASS,ADMENER)
C.4B
              CALL FEMALE (ADFPOP,FMASS,ADFENER)
C.4C
              CALL JUVENIL (JPOP,JMASS,JENER)
C.4D
           MALETOT = MALETOT + ADMENER
            FEMTOT = FEMTOT + ADFENER
            JUVTOT = JUVTOT + JENER
           TOTMASS = MMASS + FMASS + JMASS
           TOTPOP  = ADMPOP + ADFPOP + JPOP
           TOTENER = ADMENER + ADFENER + JENER
           YEAREN  = YEAREN + TOTENER
             ADMPOP = ADMPOP + 0.5*NEWPOP
             ADFPOP = ADFPOP + 0.5* NEWPOP
C.5
          WRITE(6,100) D,DAY,AVGTEMP,AVGWIND,TOTPOP,TOTMASS,TOTENER,
     2ADMENER,ADFENER,JENER
          WRITE(4,101)D,DAY,MALEKJ,FEMKJ,JUVKJ(1),JUVKJ(2),JUVKJ(3)
 100      FORMAT(F4.0,X,F4.0,X,2F5.1,X,F5.1,X,F5.1,X,F8.1,X,3F8.1)
 101      FORMAT(F4.0,X,F4.0,5F12.1)
        END DO
C.6
              PRINT*,YEAREN,' kJ/KM^2*YEAR = POPULATION ENERGY'
              PRINT*,MALETOT,' kJ/KM^2*YEAR = AD. MALE POPUL. ENERGY'
              PRINT*,FEMTOT,' kJ/KM^2*YEAR = AD. FEMALE POPUL. ENERGY'
              PRINT*,JUVTOT,' kJ/KM^2*YEAR = JUVENILE POPUL. ENERGY'
           END
C
C
C
```

```
C*****************************************************************
C*****************************************************************
C********** S E C O N D - T I E R   S U B R O U T I N E S *********
C*****************************************************************
C*****************************************************************
C
C
C
C*****************************************************************
C*************** A D U L T   M A L E   E N E R G Y **************
C*****************************************************************
        SUBROUTINE MALE (ADMPOP,MMASS,ADMENER)
C
C
         REAL D,DAY,DAYLEN,TEMP(2),WIND(2)
         REAL ADMPOP,MMASS,ADMENER,MALEKJ
         REAL ADMTREG,ADMSDA,ADMPRO,ADMACTV,EN1ADM
         REAL ADMMASS,OLDMMASS
         INTEGER MFLAG
         COMMON /DAYS/ DAY,DAYLEN
         COMMON /ADM/ MALEKJ,MFLAG,ADMMASS
         COMMON /STEP/ D
         COMMON /ENVIRON/ TEMP,WIND
         COMMON /M/ OLDMMASS
C-------------------------------------------------------------
C THIS SUBROUTINE AMASSES AND DISTRIBUTES INFORMATION FOR THE ADULT
C MALE SEGMENT OF THE POPULATION.
C
C SUBROUTINES ARE CALLED THAT CALCULATE PER DAY :
C       1. ADSURV  = CURRENT POPULATION DENSITY (ANIMALS/KM^2)
C                    USING A DAILY MORTALITY RATE.
C       2. ADMPROD = CURRENT BODY MASS (KG) AND PRODUCTION ENERGY
C                      (KJ/KG*DAY). ADULT PRODUCTION IS PRIMARILY AS
C                      FAT GAIN/LOSS.
C       3. ADTHERM = MAINTENANCE + THERMOREGULATORY ENERGY (KJ/KG*DAY)
C               PER INDIVIDUAL AFTER SUBSTITUTION BY SDA.
C       4. ACTIVE  = ENERGY OF ACTIVITY (KJ/KG*DAY) PER INDIVIDUAL
C
C 5.   DAILY TOTALS ARE CALCULATED PER CAPITA:
C
C              EN1ADM  = ENERGY USE FOR 1 ADULT MALE (KJ/KG*DAY)
C                 (The sum of energy for maint. + thermoreg (ADMTREG),
C                 production (ADMPRO and activity (ADMACTV).
C
C              MALEKJ = ENERGY USE PER ONE MALE (kJ/DAY)
C                using ADMMASS (mass for 1 adult male, KG)
C
C                        **************
C 6.           MASS SPECIFIC ENERGY VALUES FOR MALES ARE PRINTED
C                              IN FILE "ADMIND.OUT"
C              IF USER HAS REQUESTED PRINTOUT IN MAIN PROGRAM.
C
```

```
C               VALUES IN PRINTOUT FROM LEFT TO RIGHT:
C
C       D        = LINE NUMBER (1-365)
C       DAY      = DAY (65-365, THEN 1-64)
C       ENIADM   = ENERGY FOR 1 ADULT MALE (kJ/KG*DAY)
C       ADMPOP   = MALE POPULATION DENSITY (NUMBER/KM^2*DAY)
C       ADMMASS  = MASS OF 1 MALE (kg)
C       ADMTREG  = ENERGY OF MAINTEN. + THERMOREG. (kJ/KG*DAY)
C       ADMSDA   = SDA (kJ/KG*DAY)
C                       This is residual SDA that was not used to
c                       substitute for thermoregulatory cost.
C       ADMPRO   = PRODUCTION ENERGY (non-reproductive, kJ/KG*DAY)
C       ADMACTV  = ACTIVITY ENERGY PER INDIVIDUAL (kJ/KG*DAY)
C
C 7.   DAILY TOTALS ARE CALCULATED FOR ALL INDIVIDUALS:
c    Total energy demand on the environment includes all SDA.
C
C               MMASS    = MASS OF ALL ADULT MALES (KG/KM^2*DAY)
C               ADMENER  = ENERGY OF ALL ADULT MALES (KJ/KM^2*DAY)
C-------------------------------------------------------------------
C.1
          CALL ADSURV (ADMPOP)
C.2
          CALL ADMPROD (DAY,ADMMASS,ADMPRO)
C.3
          CALL ADTHERM (ADMTREG,ADMSDA)
C.4
          CALL ACTIVE (ADMMASS,ADMACTV)
C.5
        EN1ADM = ADMTREG+ADMPRO+ADMACTV
        MALEKJ = EN1ADM*ADMMASS
C.6
       IF (MFLAG.NE.0.0) THEN
         WRITE(7,200)D,DAY,EN1ADM,ADMPOP,ADMMASS,ADMTREG,ADMSDA,
    2ADMPRO,ADMACTV
       END IF
  200    FORMAT(F4.0,X,F4.0,X,F8.1,F5.1,F5.2,4F8.1)
C.7
             MMASS = ADMMASS*ADMPOP
           ADMENER = (EN1ADM+ADMSDA)*MMASS
       END
C
C
C
C*******************************************************************
C************* A D U L T    F E M A L E    E N E R G Y ************
C*******************************************************************
      SUBROUTINE FEMALE (ADFPOP,FMASS,ADFENER)
       REAL D,DAY,DAYLEN,TEMP(2),WIND(2)
       REAL ADFPOP,FMASS,ADFENER,FEMKJ
       REAL ADFTREG,ADFSDA,ADFPRO,ADFACTV
       REAL ADFMASS,OLDFMASS,MILK(3),MKENER(3)
```

```
        REAL GD,LD,GESTEN(3),LACTEN(3),L1,L2,L3
        REAL GEST,LACT,EN1ADF,ADF
        INTEGER LN,FFLAG
        PARAMETER (L1=4.3,L2=6.2,L3=3.8)
        COMMON /DAYS/ DAY,DAYLEN
        COMMON /ENVIRON/ TEMP,WIND
        COMMON /ADF/ FEMKJ,FFLAG,ADFMASS
        COMMON /STEP/ D
        COMMON /F/ OLDFMASS
     COMMON/ MK/ MKENER
C------------------------------------------------------------------
C THIS SUBROUTINE AMASSES AND DISTRIBUTES INFORMATION FOR THE ADULT
C FEMALE SEGMENT OF THE POPULATION.
C
C SUBROUTINES ARE CALLED THAT CALCULATE FOR EACH DAY::
C       1. ADSURV   = CURRENT POPULATION DENSITY (ANIMALS/KM^2)
C                     USING A DAILY MORTALITY RATE
C       2. ADFPROD  = CURRENT BODY MASS (KG) AND PRODUCTION ENERGY
C                       (kJ/KG*DAY).  ADULT PRODUCTION IS CHIEFLY
C                       AS FAT GAIN/LOSS.
C       3. GESTATE  = ENERGY OF GESTATION (KJ/KG*DAY) PER INDIV. FEMALE
C                     CALCULATED FOR EACH LITTER - GESTEN(LN) - AND FOR
C                     ALL LITTERS COMBINED (GEST). LN = litter #1,2or3.
C       4. LACTATE  = ENERGY OF LACTATION (KJ/KG*DAY) PER INDIV. FEMALE
C                     CALCULATED FOR EACH LITTER - LACTEN(LN) - AND FOR
C                     ALL LITTERS COMBINED (LACT).
C               Note that gestation and lactation subroutines are
c               called at first conception and parturition dates,
c               respectively, for each of the 3 litters.
C
C       5. ADTHERM  = MAINTENANCE + THERMOREGULATORY ENERGY (KJ/KG*DAY)
C               PER INDIVIDUAL AFTER SUBSTITUTION BY SDA.
C       6. ACTIVE   = ENERGY OF ACTIVITY PER INDIVIDUAL (KJ/KG*DAY)
C
C 7.  DAILY TOTALS ARE CALCULATED PER CAPITA:
C
C            EN1ADF  = ENERGY USE FOR 1 ADULT FEMALE (KJ/KG*DAY)
C                 (The sum of energy for maint. + thermoreg. (ADFTREG),
c                 production (ADFPRO), activity (ADFACTV),
c                 gestation (GEST) and lactation (LACT).
C
C           FEMKJ = ENERGY USE PER ONE FEMALE (kJ/DAY)
C                  using ADFMASS (mass of 1 ad. female (KG)).
C
C                       ****************
C 8.            MASS SPECIFIC ENERGY VALUES FOR FEMALES ARE PRINTED
C                               IN FILE "ADFIND.OUT"
C               IF USER HAS REQUESTED PRINTOUT IN MAIN PROGRAM.
c
C               VALUES IN PRINTOUT FROM LEFT TO RIGHT ARE:
C       D      = LINE NUMBER (1-365)
C       DAY    = DAY (65-365, THEN 1-64)
```

```
C       EN1ADF  = ENERGY FOR 1 ADULT FEMALE (kJ/KG*DAY)
C       ADFPOP  = FEMALE POPULATION DENSITY (NUMBER/KM^2*DAY)
C       ADFMASS = MASS OF 1 FEMALE (KG)
C       ADFTREG = ENERGY OF MAINTENANCE + THERMOREG. (kJ/KG*DAY)
C       ADFSDA  = SDA (kJ/KG*DAY)
C                       This is residual SDA that was not used
c                       to substitute for thermoregulatory cost.
C       ADFPRO  = PRODUCTION ENERGY (non-reproductive) (kJ/KG*DAY)
C       ADFACTV = ACTIVITY ENERGY (kJ/KG*DAY)
C       GEST    = GESTATION ENERGY (kJ/KG*DAY)
C       LACT    = LACTATION ENERGY (kJ/KG*DAY)
C
C 9.    DAILY TOTALS ARE CALCULATED FOR ALL INDIVIDUALS:
c      Total energy demand on the environment includes all SDA.
C
C            FMASS = MASS OF ALL ADULT FEMALES (KG/KM^2*DAY)
C          ADFENER = ENERGY OF ALL ADULT FEMALES (KJ/KM^2*DAY)
C    MKENER(LN) = ENERGY IN MILK (KJ/KG*DAY) PER LITTER (LN)
C              (TRANSFERRED TO SUBROUTINE JUVENIL)
C
C               ADFENER IS REDUCED BY 0.52 TIMES THE ENERGY OF
C               GESTATION AND LACTATION DURING THE 3RD LITTER
C               BECAUSE ONLY 48% OF 3RD LITTER FEMALES REPRODUCED.
C               TOTAL MILK ENERGY IS ALSO REDUCED IN THE 3RD LITTER.
C----------------------------------------------------------------
C.1
           CALL ADSURV (ADFPOP)
C.2
           CALL ADFPROD (DAY,ADFMASS,ADFPRO)
C.3
                 DO LN = 1,3
                   GESTEN(LN) = 0.0
                   LACTEN(LN) = 0.0
                     MILK(LN) = 0.0
                   MKENER(LN) = 0.0
                 END DO
         IF (DAY.GE.65.0.AND.DAY.LE.106.0) THEN
           GD = DAY - 64.0
           CALL GESTATE (GD,L1,GESTEN(1),ADFMASS)
         END IF
         IF (DAY.GE.112.0.AND.DAY.LE.153.0) THEN
           GD = DAY - 111.0
           CALL GESTATE (GD,L2,GESTEN(2),ADFMASS)
         END IF
         IF (DAY.GE.157.0.AND.DAY.LE.198.0) THEN
           GD = DAY - 156.0
           CALL GESTATE (GD,L3,GESTEN(3),ADFMASS)
         END IF
           GEST = GESTEN(1)+GESTEN(2)+GESTEN(3)
C.4
         IF (DAY.GE.107.0.AND.DAY.LE.136.0) THEN
           LD = DAY - 106.0
```

```
          CALL LACTATE (LD,L1,ADFMASS,LACTEN(1),MILK(1))
        END IF
        IF (DAY.GE.154.0.AND.DAY.LE.183.0) THEN
          LD = DAY - 153.0
          CALL LACTATE (LD,L2,ADFMASS,LACTEN(2),MILK(2))
        END IF
        IF (DAY.GE.199.0.AND.DAY.LE.228.0) THEN
          LD = DAY - 198.0
          CALL LACTATE (LD,L3,ADFMASS,LACTEN(3),MILK(3))
        END IF
          LACT = LACTEN(1)+LACTEN(2)+LACTEN(3)
C.5
          CALL ADTHERM (ADFTREG,ADFSDA)
C.6
          CALL ACTIVE (ADFMASS,ADFACTV)
C.7
       EN1ADF=ADFTREG+ADFPRO+ADFACTV+GEST+LACT
       FEMKJ = EN1ADF*ADFMASS
C.8
       IF (FFLAG.NE.0.0) THEN
          WRITE(8,300)D,DAY,EN1ADF,ADFPOP,ADFMASS,ADFTREG,ADFSDA,
    2ADFPRO,ADFACTV,GEST,LACT
       END IF
 300      FORMAT(F4.0,X,F4.0,X,F7.1,F5.1,F5.2,6F7.1)
C.9
        FMASS = ADFMASS*ADFPOP
          ADF = EN1ADF + ADFSDA
      ADFENER = (ADF-0.52*(GESTEN(3)+LACTEN(3)))*FMASS
       MKENER(1) = MILK(1)*FMASS
       MKENER(2) = MILK(2)*FMASS
       MKENER(3) = MILK(3)*FMASS*0.48
       END
C
C
C
C*****************************************************************
C************** J U V E N I L E   E N E R G Y *******************
C*****************************************************************
       SUBROUTINE JUVENIL (JPOP,JMASS,JENER)
        REAL D,DAY,DAYLEN,TEMP(2),WIND(2),ADFPOP,NEWPOP
        REAL JPOP,JMASS,JENER,JUVKJ(3)
        REAL AGE(3),JUVPOP(3),JUVMASS(3),JUVPRO(3),JUVTREG(3)
        REAL JUVSDA(3),JUVACTV(3)
        REAL EN1JUV(3),COHENER(3),COHMASS(3),MKENER(3)
        INTEGER LN,JFLAG,HUDFLAG
        COMMON /DAYS/ DAY,DAYLEN
        COMMON /ENVIRON/ TEMP,WIND
        COMMON /JUV/ JUVKJ,JUVPOP,NEWPOP,ADFPOP,JFLAG
        COMMON /STEP/ D
        COMMON /MK/ MKENER
        COMMON /MANIP/ HUDFLAG
C-----------------------------------------------------------
```

```
C THIS SUBROUTINE AMASSES AND DISTRIBUTES INFORMATION FOR THE
C JUVENILE SEGMENT OF THE POPULATION.
C
C       1. VARIABLES THAT ARE LATER SUMMED ARE SET TO ZERO
C
C       2. AGE OF ANIMALS PER COHORT (1-3) ARE DETERMINED
C
C SUBROUTINES ARE CALLED THAT CALCULATE PER DAY:
C
C       3. JUVSURV    = CURRENT POPULATION DENSITY (#/KM) PER DAY
C                           NOTE:
C                       WHEN ANIMALS ARE EQUAL OR OLDER THAN 175 DAYS
C                       THEY ARE CONSIDERED TO BE NEW ADULTS (NEWPOP).
C       4. JUVPROD  = CURRENT BODY MASS (KG) AND PRODUCTION ENERGY
C                      (kJ/KG*DAY) OF GROWTH PER INDIVIDUAL.
C       5. JUVTHERM = MAINTENANCE + THERMOREGULATORY ENERGY (KJ/KG*DAY)
C                     PER INDIVIDUAL AFTER SUBSTITUTING BY SDA.
C                     ADTHERM IS CALLED FOR ANIMALS GREATER THAN
C                     115 DAYS OLD (THESE ANIMALS THERMOREGULATE
C                     AS ADULTS).
C       6. ACTIVE =   ENERGY OF ACTIVITY (KJ/KG*DAY PER INDIVIDUAL)
C                       ANIMALS UNDER 30 DAYS HAVE NEGLIGIBLE ACTIVITY
C                       AFTER LACTATION PERIOD (30 DAYS) ANIMALS ARE
C                       ASSUMED TO HAVE ACTIVITY PATTERN SIMILAR TO
C                       ADULTS (ADJUSTED FOR BODY MASS)
C
C   7.  DAILY TOTALS ARE SUMMED ON A PER CAPITA BASIS
C
C               ENIJUV(LN) = ENERGY USE PER 1 JUVENILE (kJ/KG*DAY)
C                   PER ONE LITTER PERIOD (LN) where LN = 1, 2 or 3.
C                 (The sum of energy of production [JUVPRO(LN)],
c                 maintenance + thermoregulation [JUVTREG(LN)]
C                 and activity [JUVACTV(LN)].
C
C               JUVKJ(LN) = ENERGY USE PER 1 JUVENILE (kJ/DAY)
C                       PER LITTER PERIOD, calculated by multiplying
c                       EN1JUV(LN)] times mass (kg) [JUVMASS(LN)]
C
C  8.   COHORT MASS AND ENERGY = CALCULATED, where a cohort = all
c       of the individuals born in one litter period that are alive.
c    Cohort energy demand on environment includes all of SDA.
C        Cohort energy demand on the environment is zero if cohort is
c    totally dependent on milk from does (the 1st 17 days of
c    lactation).  After day 17, energy demand not met by milk
c    is taken from the environment (see Tiemeier 1965, Martinet
c       and Demarne 1984).
C
c               COHMASS(LN)     = MASS OF COHORT (KG/COHORT*DAY)
C
c               COHENER(LN)     = COHORT ENERGY (kJ/COHORT*DAY)
C
C  9.   DAILY TOTALS ARE CALCULATED FOR ALL JUVENILES
```

```
C
C               JPOP    = POPULATION OF ALL JUVENILES (NUMBER/KM^2)
C               JMASS   = MASS OF ALL JUVENILES (KG/KM^2)
C               JENER   = ENERGY OF ALL JUVENILES (KJ/KM^2)
C
C                       ****************
C 10.   THREE FILES WITH ENERGY VALUES ARE PRINTED OUT IF USER
C       HAS REQUESTED PRINTOUT IN MAIN PROGRAM.
c
C       MASS SPECIFIC ENERGY VALUES FOR LITTER 1, LITTER 2,
C       AND LITTER 3 ARE PRINTED IN "JUVIND1.OUT", "JUVIND2.OUT",
C       AND "JUVIND3.OUT', RESPECTIVELY.  VALUES IN THESE FILES
C       FROM LEFT TO RIGHT FOLLOW (note LN = litter number):
C
C       D               = LINE NUMBER (1-365)
C       DAY             = DAY (65-365, THEN 1-64)
C       EN1JUV(LN)      = ENERGY OF 1 JUVENILE IN THE LITTER
C                         (kJ/KG*DAY)
C       JUVPOP(LN)      = POPULATION OF JUVENILES IN LITTER
C                                 (NUMBER/KM^2)
C       JUVMASS(LN)     = MASS OF 1 JUVENILE IN LITTER (KG)
C       JUVTREG(LN)     = MAINTENANCE + THERMOREGULATORY ENERGY
C                         PER 1 JUV. PER LITTER (kJ/KG*DAY)
C       JUVSDA(LN)      = SDA PER 1 JUV. PER LITTER (kJ/KG*DAY)
C                         This is residual SDA that was not used
c                         to substitute for thermoregulatory cost.
C       JUVPRO(LN)      = PRODUCTION ENERGY PER 1 JUVENILE PER
C                         LITTER (kJ/KG*DAY)
C       JUVACTV(LN)     = ACTIVITY ENERGY PER 1 JUVENILE PER
C                         LITTER (kJ/KG*DAY)
C
C 1.
         NEWPOP = 0.0
          JENER = 0.0
           JPOP = 0.0
          JMASS = 0.0
C.2
           AGE(1) = DAY - 107.0
           AGE(2) = DAY - 154.0
           IF (DAY.GE.199.0) THEN
             AGE(3) = DAY - 199.0
           ELSE
             AGE(3) = DAY + 166.0
           END IF
C SUBROUTINES:
        DO LN = 1,3
          IF (AGE(LN).LT.0.0.OR.AGE(LN).GT.175.0) THEN
             JUVTREG(LN) = 0.0
              JUVSDA(LN) = 0.0
              JUVPRO(LN) = 0.0
             JUVACTV(LN) = 0.0
             JUVMASS(LN) = 0.0
```

```
              JUVPOP(LN) = 0.0
          ELSE
C.3
            CALL JUVSURV (ADFPOP,LN,AGE(LN),JUVPOP(LN))
                IF (AGE(LN).EQ.175.0) THEN
                  NEWPOP = NEWPOP + JUVPOP(LN)
                END IF
C.4
           CALL JUVPROD (AGE(LN),JUVPRO(LN),JUVMASS(LN))
C.5
             IF (AGE(LN).LE.115.0) THEN
              CALL JUVTHERM (DAYLEN,TEMP,AGE(LN),JUVTREG(LN),JUVSDA(LN))

             ELSE
              CALL ADTHERM (JUVTREG(LN),JUVSDA(LN))
             END IF
C.6
          IF (AGE(LN).GT.30.0) THEN
              CALL ACTIVE (JUVMASS(LN),JUVACTV(LN))
          END IF
          END IF
C.7
      EN1JUV(LN)=JUVTREG(LN)+JUVPRO(LN)+JUVACTV(LN)
      JUVKJ(LN) = EN1JUV(LN)*JUVMASS(LN)
C.8
             COHMASS(LN) = JUVPOP(LN)*JUVMASS(LN)
             COHENER(LN) = (EN1JUV(LN)+JUVSDA(LN))*COHMASS(LN)
         IF (AGE(LN).GE.0.0.AND.AGE(LN).LE.29.0) THEN
              IF (AGE(LN).LE.17.0) THEN
                   COHENER(LN) = 0.0
              ELSE
                  COHENER(LN) = COHENER(LN) - MKENER(LN)
              END IF
         END IF
C.9
          JPOP = JPOP + JUVPOP(LN)
         JMASS = JMASS + COHMASS(LN)
         JENER = JENER + COHENER(LN)
C
  400   END DO
C.10
        IF (JFLAG.NE.0) THEN
         WRITE(1,410)D,DAY,EN1JUV(1),JUVPOP(1),JUVMASS(1),JUVTREG(1),
     2JUVSDA(1),JUVPRO(1),JUVACTV(1)
         WRITE(2,410)D,DAY,EN1JUV(2),JUVPOP(2),JUVMASS(2),JUVTREG(2),
     2JUVSDA(2),JUVPRO(2),JUVACTV(2)
         WRITE(3,410)D,DAY,EN1JUV(3),JUVPOP(3),JUVMASS(3),JUVTREG(3),
     2JUVSDA(3),JUVPRO(3),JUVACTV(3)
        END IF
  410  FORMAT(F4.0,X,F4.0,X,F8.1,F5.1,F5.2,4F8.1)
               END
C
```

```
C
C
C**********************************************************************
C********************* T H I R D - T I E R **************************
C******************** S U B R O U T I N E S *************************
C**********************************************************************
C
C
C
C************************************************************************
C********* A D U L T   P O P U L A T I O N   D E N S I T Y *********
C************************************************************************
        SUBROUTINE ADSURV (POPDEN)
             REAL POPDEN
C--------------------------------------------------------------
C THIS SUBROUTINE CALCULATES THE POPULATION DENSITY OF ADULT
C JACKRABBITS BASED ON DEMOGRAPHIC STUDIES BY L. C. STODDART.
C POPDEN    = DENSITY OF ADULT MALES <OR> ADULT FEMALES
C               (WHICHEVER IS ACCESSING THE ROUTINE)
C DAILY MORTALITY RATE IS 0.0058
C OUPUT:
C  ADPOP = POPULATION DENSITY OF ADULTS (ANIMALS/KM^2*DAY)
C-----------------------------------------------------------------------
             POPDEN = POPDEN - (POPDEN*0.0058)
             END
C
C
C
C***********************************************************************
C***** J U V E N I L E   P O P U L A T I O N   D E N S I T Y *****
C***********************************************************************
        SUBROUTINE JUVSURV (ADFPOP,LN,AGE,JUVPOP)
         REAL ADFPOP, AGE,JUVPOP
         REAL REPOUT(3)
         INTEGER LN
C--------------------------------------------------------------------
C THIS SUBROUTINE COMPUTES JUVENILE POPULATION DENSITY AND USES
C A DAILY MORTALITY RATE DERIVED FROM LONG-TERM STUDIES OF
C JACKRABBITS BY L. C. STODDART (UTAH STATE UNIVERSITY, LOGAN, UT).
C AGE         = AGE IN DAYS OF JUVENILE
C REPOUT(3)  = REPRODUCTIVE OUTPUT PER LITTER (LN), WHERE REPRODUCTIVE
C             OUTPUT IS: Litter Size * Fraction of Reproductive Females
C               FOR LN = 1     4.3    *     1.0
C               FOR LN = 2     6.2    *     1.0
C               FOR LN = 3     3.8    *     0.48
C                   (Where LN = litter number)
C ADFPOP     = DENSITY PER KM^2 OF ADULT FEMALES
C DAILY MORTALITY RATES FOR JUVENILES ARE MODELED TO BE:
C       1. HIGHER FOR YOUNG ANIMALS        = 0.0062
c       2. LOWER FOR ANIMALS > 115 DAYS OLD = 0.0058
C OUTPUT:
C  JUVPOP = POPULATION DENSITY OF JUVENILES PER COHORT (1 - 3)
```

```
C          (ANIMALS/KM^2*DAY)
C-------------------------------------------------------------
C INITIAL INTRO. OF JUVENILES INTO POPUL. BY PARTURITION:
          IF (AGE.LT.1.0) THEN
                REPOUT(1) = 4.3
                REPOUT(2) = 6.2
                REPOUT(3) = 1.8
            JUVPOP = ADFPOP*REPOUT(LN)
C1.
          ELSE IF (AGE.GE.1.0.AND.AGE.LE.115.0) THEN
            JUVPOP = JUVPOP - JUVPOP*0.0062
C2.
          ELSE
            JUVPOP = JUVPOP - JUVPOP*0.0058
          END IF
          END
C
C
C
C****************************************************************
C*** A D U L T   T H E R M O R E G U L A T O R Y   E N E R G Y ***
C****************************************************************
        SUBROUTINE ADTHERM(ADTREG,ADSDA)
               REAL TEMP(2),WIND(2)
               REAL DAY,DAYLEN
               REAL SMR,X,Y,TR(2),ADTREG,ADSDA
               REAL SMRW,SMRS,TW(2),TS(2)
               REAL DAYHR,NITHR
               INTEGER P
               COMMON /ENVIRON/ TEMP,WIND
               COMMON /DAYS/ DAY,DAYLEN
C---------------------------------------------------------------
C THIS SUBROUTINE COMPUTES THE THERMOREGULATORY ENERGY AND SDA
C        FOR ADULT ANIMALS, BASED ON:
C  TEMP(P) = MEAN TEMPERATURE FOR DAY(P=1) AND NIGHT(P=2)
C  WIND(P) = MEAN WIND SPEED  FOR DAY(P=1) AND NIGHT(P=2)
C  DAYLEN  = DAYLENGTH
C  SMR     = STANDARD METABOLIC RATE (kJ/KG*DAY) FOR SUMMER, WINTER
C            OR MOLT PERIODS (AN AVERAGE OF SUMMER AND WINTER RATES).
C            Summer (Day 136-279), Fall Molt (Day 280-324),
c            Winter (Day 325-365,1-90), Spring Molt (Day 91-135).
C TR (P)   = ENERGY COST (KJ/KG/DAY) FOR P = 1 (DAY) AND P = 2 (NIGHT)
C            PRIOR TO ADJUSTING FOR # HOURS IN DAY AND IN NIGHT.
c            Separate equations describe energy use with wind or with
c            no wind (based on oxygen consumption experiments).
C            TR(P) IS A MEAN OF WINTER VS. SUMMER DURING MOLT PERIODS.
C DAYHR   = FRACTION OF DAY THAT IS DAYTIME
C NITHR   = FRACTION OF DAY THAT IS NIGHTTIME
C SDA     = SPECIFIC DYNAMIC ACTIVITY (HEAT INCREMENT).  SDA
C           OCCURS DURING FEEDING TIMES (BRODY 1964).  IF FEEDING
C           IS ONLY OCCASIONAL, SDA CANNOT BE DETECTED.  THEREFORE, SDA
C           IS CALCULATED ONLY DURING NIGHTTIME (FEEDING HOURS).  SDA
```

```
C           IS ASSUMED TO SUBSTITUTE FOR THERMOREGULATORY COST BELOW
C           THE THERMONEUTRAL ZONE.
C
C  OUTPUT:
C ADTREG (KJ/KG*DAY) FOR THERMOREGULATION
C ADSDA  (KJ/KG*DAY) FOR SPECIFIC DYNAMIC ACTIVITY
c              This is residual SDA left after reducing thermoreg.
c               cost.
C------------------------------------------------------------------
       DO P = 1,2
C   WINTER
         IF (DAY.LE.91.0.OR.DAY.GE.330.0) THEN
               SMR = 299.02
           IF (WIND(P).NE.0.0) THEN
       TR(P)=314.0-1.91*TEMP(P)+69.0*WIND(P)**0.5-4.57*TEMP(P)*
     2WIND(P)**0.5
           ELSE
             IF (TEMP(P).LT.-6.0) THEN
                TR(P) = 258.0 - 6.94*TEMP(P)
             ELSE
                TR(P) = SMR
             END IF
           END IF
C    SUMMER
        ELSE IF (DAY.GE.139.0.AND.DAY.LE.282.0) THEN
                  SMR = 244.04
             IF (WIND(P).NE.0.0) THEN
       TR(P)=314.0-2.76*TEMP(P)+146.0*WIND(P)**0.5-4.92*TEMP(P)*
     2WIND(P)**0.5
             ELSE
                IF (TEMP(P).LT.11.0) THEN
                   TR(P) = 335.0 - 7.79*TEMP(P)
                ELSE
                   TR(P) = SMR
                END IF
             END IF
        ELSE
C  MOLT
               SMRW = 299.02
           IF (WIND(P).NE.0.0) THEN
       TW(P)=314.0-1.91*TEMP(P)+69.0*WIND(P)**0.5-4.57*TEMP(P)*
     2WIND(P)**0.5
           ELSE
             IF (TEMP(P).LT.-6.0) THEN
                TW(P) = 258.0 - 6.94*TEMP(P)
             ELSE
                TW(P) = SMR
             END IF
           END IF
                  SMRS = 244.04
             IF (WIND(P).NE.0.0) THEN
       TS(P)=314.0-2.76*TEMP(P)+146.0*WIND(P)**0.5-4.92*TEMP(P)*
```

```
     2WIND(P)**0.5
              ELSE
                 IF (TEMP(P).LT.11.0) THEN
                    TS(P) = 335.0 - 7.79*TEMP(P)
                 ELSE
                    TS(P) = SMR
                 END IF
              END IF
            TR(P) = (TW(P) + TS(P))*0.5
            SMR = (SMRW + SMRS)*0.5
           END IF
        END DO
              SDA = SMR*0.27
              X = TR(2) - SMR
              IF (X.LE.SDA) THEN
                 TR(2) = SMR
              ELSE
                 TR(2) = TR(2) - SDA
              END IF
              Y = SDA - X
              IF (Y.LE.0.0)THEN
                  SDA = 0.0
              ELSE
                  SDA = Y
              END IF
           DAYHR = DAYLEN/24.0
           NITHR = (24.0-DAYLEN)/24.0
           ADTREG = TR(1)*DAYHR + TR(2)*NITHR
           ADSDA = SDA*NITHR
                END
C
C
C
C********************************************************************
C* J U V E N I L E   T H E R M O R E G U L A T O R Y   E N E R G Y *
C********************************************************************
        SUBROUTINE JUVTHERM (DAYLEN,TEMP,AGE,JUVTREG,JUVSDA)
            REAL DAYLEN,TEMP(2),AGE
            REAL TR(2),SMR,SDA,JUVTREG,JUVSDA,X,Y
            REAL DAYHR,NITHR
            INTEGER P,HUDFLAG
            PARAMETER(SMR=244.04)
            COMMON /MANIP/ HUDFLAG
C--------------------------------------------------------------------
C THIS SUBROUTINE COMPUTES THE THERMOREGULATORY ENERGY
C         AND SDA OF JUVENILES,  BASED ON:
C TEMP(P)    = MEAN TEMP. FOR DAYS(P=1) AND NIGHTS(P=2)
C AGE        = AGE IN DAYS OF ANIMAL
C SMR        = STANDARD METABOLIC RATE FOR SUMMER ANIMALS (KJ/KG)
C TR(P)      = ENERGY COST FOR P = 1 (DAY) AND P = 2(NIGHT)
C              PRIOR TO ADJUSTING FOR #HOURS IN DAY AND NIGHT.
C               Energy use is high in the first week of life and
```

```
c              declines with age (based on 02 consumption expts.)
C DAYHR      = FRACTION OF DAY THAT IS DAYTIME
C NITHR      = FRACTION OF DAY THAT IS NIGHTTIME
C SDA        = SPECIFIC DYNAMIC ACTIVITY (SEE EXPLANATION UNDER
C              "ADULT THERMOREGULATORY ENERGY" SUBROUTINE.
C
C          IF REQUESTED AT PROGRAM START, HUDDLING CAN BE
C          SIMULATED BASED ON A MAX. OF 40% REDUCTION AT
C          0 C (ESTIMATED FROM STUDIES OF TROJAN (1969)
C OUTPUT:
C JUVSDA   = SDA PER JUVENILE (KJ/KG*DAY)
C              This is residual SDA after reducing thermoregul. cost.
C JUVTREG = JUVENILE THERMOREG. ENERGY (KJ/KG*DAY)
C-------------------------------------------------------------------
       DO P = 1,2
            IF (AGE.LT.7.0) THEN
               TR(P)=3423.0-37.2*TEMP(P)-235.0*AGE
            ELSE
               TR(P)=1632.0-7.74*TEMP(P)-267.0*LOG(AGE)
            END IF
              IF (HUDFLAG.NE.0) THEN
                 TR(P) = TR(P)*(0.6 + 0.01*TEMP(P))
              END IF
        END DO
              SDA = SMR*0.27
              X = TR(2) - SMR
              IF (X.LE.SDA) THEN
                  TR(2) = SMR
              ELSE
                  TR(2) = TR(2) - SDA
              END IF
              Y = SDA - X
              IF (Y.LE.0.0) THEN
                 SDA = 0.0
               ELSE
                  SDA = Y
               END IF
            DAYHR = DAYLEN/24.0
            NITHR = (24.0 - DAYLEN)/24.0
            JUVTREG = TR(1)*DAYHR + TR(2)*NITHR
            JUVSDA = SDA*NITHR
                 END
C
C
C
C*******************************************************************
C************** A C T I V I T Y   E N E R G Y *******************
C*******************************************************************
        SUBROUTINE ACTIVE (MASS,ACTIVEN)
         REAL ACTIVEN,DAY,DAYLEN,KJKGKM,DIST
         REAL HRSACTV,MASS
         COMMON /DAYS/ DAY,DAYLEN
```

```
C---------------------------------------------------------------
C THIS SUBROUTINE CALCULATES THE ENERGY OF ACTIVITY BASED UPON:
C  KJKGKM  = KJ PER KG PER KM MOVED BASED ON EQN. OF TAYLOR AND
C            HEGLUND (1982).  ASSUMES 20.1 KJ/ l O2.
C  HRSACTV = #HOURS JACKRABBITS ARE POTENTIALLY ACTIVE (ACTIVE PHASE)
C            FROM TELEMETRY DATA AND DAYLENGTH IN WYOMING.
C                Active phase is a linear function of daylength.
C DIST     = DISTANCE MOVED BY JACKRABBITS DURING A 1 HOUR PERIOD,
C              (KM/HOUR) Total km moved in all movement bouts in 1 hr.
C                 BASED ON OBSERVATIONS AT MILLVILLE, UT
C
C OUTPUT:
C ACTIVEN  = ENERGY OF ACTIVITY (KJ/KG*DAY)
C----------------------------------------------------------------
        KJKGKM = 10.7*MASS**-0.316
        HRSACTV = 24.0 - (3.11 + 0.814*DAYLEN)
             IF (DAY.LE.31.0.OR.DAY.GE.133.0) THEN
                DIST = 0.26
             ELSE IF (DAY.GE.32.0.AND.DAY.LE.64.0) THEN
               DIST = -1.11 + 0.0442*DAY
             ELSE IF (DAY.GE.65.0.AND.DAY.LE.112.0) THEN
                DIST = 1.76
             ELSE
               DIST = 9.76 - 0.071*DAY
             END IF
        ACTIVEN = KJKGKM*DIST*HRSACTV
             END
C
C
C
C*******************************************************************
C**** A D U L T   M A L E   P R O D U C T I O N   E N E R G Y ****
C*******************************************************************
        SUBROUTINE ADMPROD (DAY,ADMMASS,ADMPRO)
           REAL DAY,ADMMASS,ADMPRO,ADCONV,ADEFF
           REAL OLDMASS,INCPRO
           PARAMETER (ADCONV=6276.0,ADEFF= 0.60)
           COMMON /M/ OLDMASS
C-------------------------------------------------------------------
C THIS SUBROUTINE CALCULATES ADULT MALE PRODUCTION ENERGY AND
C BODY MASS, BASED ON:
C    ADCONV = ENERGY CONVERSION FACTOR (KJ/KG)
c    ADEFF  = ADULT PRODUCTION EFFICIENCY (UNITLESS)
C            (Assumes body mass change primarily by fat gain/loss).
C   OLDMASS = MASS ON PREVIOUS DAY (KG)
C  ADMMASS  = MASS ON CURRENT DAY (KG) BASED ON FIELD BODY MASSES OF
C               JACKRABBITS COLLECTED IN WYOMING.
C   INCPRO  = INCREMENTAL INCREASE IN MASS FROM PREVIOUS TO CURRENT DAY
C               (Kg increase per kg of body mass)
C
C OUTPUT:
C  ADMPRO  =  ADULT MALE PRODUCTION ENERGY (KJ/KG*DAY)
```

```
C  ADMMASS =  ADULT BODY MASS (KG/DAY)
C---------------------------------------------------------------
           IF (DAY.GE.240.0.AND.DAY.LE.282.0) THEN
                 ADMMASS = 2.1842 +0.00233*DAY
           ELSE IF (DAY.GE.283.0.AND.DAY.LE.351.0) THEN
                 ADMMASS = 3.2492 - 0.00145*DAY
           ELSE
               ADMMASS = 2.74
           END IF
C
           IF (DAY.EQ.65.0) THEN
            INCPRO = 0.0
           ELSE
            INCPRO = (ADMMASS - OLDMASS)/ADMMASS
           END IF
             ADMPRO= INCPRO*ADCONV/ADEFF
           OLDMASS = ADMMASS
             END
C
C
C
C****************************************************************
C*** A D U L T   F E M A L E   P R O D U C T I O N   E N E R G Y ***
C****************************************************************
        SUBROUTINE ADFPROD (DAY,ADFMASS,ADFPRO)
           REAL DAY,ADFMASS,ADFPRO
           REAL ADCONV,ADEFF,OLDMASS,INCPRO
           PARAMETER (ADCONV=6276.0,ADEFF=0.60)
           COMMON /F/ OLDMASS
C---------------------------------------------------------------
C THIS SUBROUTINE CALCULATES ADULT FEMALE BODY MASS AND PRODUCTION
C ENERGY BASED ON:
C ADCONV        = ENERGY CONVERSION FACTOR (KJ/KG)
C ADEFF         = ADULT PRODUCTION EFFICIENCY (UNITLESS)
C                  (Assumes body mass change primarily as fat gain/loss)
C               = OLDMASS = PREVIOUS MASS OF FEMALES (KG)
C ADFMASS       = MASS ON FIELD CURRENT DAY (KG) BASED ON FIELD
C                 BODY MASSES OF JACKRABBITS COLLECTED IN SW WYOMING.
C INCPRO        = INCREMENTAL MASS INCREASE FROM PREVIOUS TO CURRENT DAY
C                 (Kg increase per kg of body mass).
C
C
C OUTPUT:
C ADFPRO = ADULT FEMALE PRODUCTION ENERGY (KJ/KG*DAY)
C ADFMASS =  ADULT BODY FMASS (KG/DAY)
C-------------------------------------------------------------
        IF(DAY.GE.30.0.AND.DAY.LE.64.0) THEN
             ADFMASS = 2.821 + 0.00583*DAY
          ELSE IF (DAY.GE.65.0.AND.DAY.LE.204.0) THEN
             ADFMASS = 3.2
          ELSE IF (DAY.GE.205.0.AND.DAY.LE.240.0) THEN
             ADFMASS = 4.358 - 0.00568*DAY
```

```
          ELSE
            ADFMASS = 2.99
          END IF
           IF (DAY.GE.65.0.AND.DAY.LE.204.0) THEN
                INCPRO = 0.0
           ELSE
               INCPRO = (ADFMASS - OLDFMASS)/ADFMASS
           END IF
                ADFPRO = INCPRO*ADCONV/ADEFF
           OLDFMASS = ADFMASS
           END
C
C
C
C*****************************************************************
C******* J U V E N I L E   P R O D U C T I O N   E N E R G Y *******
C*****************************************************************
        SUBROUTINE JUVPROD (AGE,JUVPRO,JUVMASS)
                REAL AGE,JYIELD(200),JINCPRO
                REAL JCONV,JEFF,JUVPRO,JUVMASS
                INTEGER JAGE
                PARAMETER (JCONV=3400.0,JEFF=0.70)
C--------------------------------------------------------------
C THIS SUBROUTINE COMPUTES THE PRODUCTION ENERGY AND MASS
C OF EACH JUVENILE FROM EACH LITTER (1-3), BASED ON:
C   AGE    = AGE IN DAYS OF JUVENILE (= AGE OF COHORT)
C   JYIELD(JAGE) =  MASS OF ONE JUVENILE (KG/DAY)
C            (where JAGE is current day or previous day (DAY - 1)
c           GROWTH IS BASED ON THE VON BERTALANFFY SIGMOIDAL EQUATION
C                 FIT TO JUVENILE AGE-BODY MASS DATA.
C   JINCPRO  = INCREMENTAL MASS CHANGE (KG)
C                (FROM DAY-1  TO   CURRENT DAY)
C               (Kg increase per kg of body mass)
C     JCONV  = ENERGY CONVERSION FACTOR (KJ/KG)
C     JEFF   = JUVENILE GROWTH EFFICIENCY (UNITLESS FRACTION)
C
C   OUTPUT:
C   JUVPRO   = ENERGY OF JUVENILE PRODUCTION (KJ/KG*DAY)
C  JUVMASS   = MASS PER JUVENILE (KG/DAY)
C--------------------------------------------------------------
            DO JAGE = AGE-1,AGE
     JYIELD(JAGE)=2.893*((1.0-((EXP(-0.019*(JAGE-39.05)))/3.0))**3.0)
            END DO
         IF (AGE.GT.0.0) THEN
             JINCPRO = (JYIELD(AGE) - JYIELD(AGE-1))/JYIELD(AGE)
             JUVPRO = JINCPRO*JCONV/JEFF
         ELSE
             JUVPRO = 0.0
         END IF
             JUVMASS = JYIELD(AGE)
            END
C
```

```
C
C
C*****************************************************************
C************ G E S T A T I O N   E N E R G Y********************
C*****************************************************************
        SUBROUTINE GESTATE (GD,LITSIZ,GESTEN,ADFMASS)
         REAL GD,GESTEN,LITSIZ
         REAL FETPROD,FETMASS,ADFMASS
         REAL FETCONV,FETEFF,ALLPRO,OLDKG,KGNOW,INCPRO
         PARAMETER (FETCONV=3400.0,FETEFF=0.4,ALLPRO=1.25)
C---------------------------------------------------------------
C THIS SUBROUTINE CALCULATES THE ENERGY OF GESTATION PER LITTER
C PERIOD (1-3), BASED ON:
C GD     = GESTATION DAY (1-42)
C LITSIZ       = LITTER SIZE
C FETCONV      = ENERGY CONVERSION FACTOR (KJ/KG)
C FETEFF       = FETAL GROWTH EFFICIENCY (A FRACTION)
C ALLPRO       = FACTOR TO ADJUST FOR PLACENTAL GROWTH AND OTHER
C                PRODUCTION THAT IS ACCESSORY TO FETAL GROWTH
C   OLDKG      = KG PER FETUS ON PREVIOUS DAY
C   KGNOW      = KG PER FETUS ON CURRENT DAY
C INCPRO       = INCREMENT OF BODY MASS GAIN FROM PREVIOUS TO CURRENT DAY
C                (KG)
C FETMASS      = MASS OF LITTER (KG)
C FETPROD      = ENERGY FOR FETAL MASS PRODUCTION (kJ/KG*DAY)
C
C       FETAL GROWTH FUNCTION IS EXPONENTIAL FROM 0.005 KG AT BIRTH
C       TO 0.08 KG AT PARTURITION.  EXPONENTIAL FUNCTION DERIVED FROM
C       SNOWSHOE HARE FETAL GROWTH (BOOKHOUT 1965) AND PREDICTS A
C       BODY MASS GAIN OF 5 GRAMS/DAY AT PARTURITION.
C
C OUTPUT:
C GESTEN       = ENERGY OF GESTATION (KJ/KG*DAY) PER LITTER
C ADFMASS      = MASS OF REPRODUCTIVE FEMALE (KG)
C---------------------------------------------------------------
                 OLDKG = 0.005*EXP(0.065*(GD-1.0))
                 KGNOW = 0.005*EXP(0.065*GD)
               FETMASS = KGNOW*ALLPRO*LITSIZ
               ADFMASS = ADFMASS + FETMASS
                INCPRO = KGNOW - OLDKG
               FETPROD = INCPRO*ALLPRO*FETCONV*LITSIZ/ADFMASS
               GESTEN  = FETPROD/FETEFF
        END
C
C
C
C*****************************************************************
C************ L A C T A T I O N   E N E R G Y*******************
C*****************************************************************
        SUBROUTINE LACTATE (LD,LITSIZ,ADFMASS,LACTEN,MILK)
         REAL LD,ADFMASS,LACTEN,LITSIZ,MILK
         REAL MLKENER,LACT,LACTEFF
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```
      PARAMETER (LACTEFF = 0.65)
C------------------------------------------------------------------
C THIS SUBROUTINE CALCULATES LACTATION ENERGY PER FEMALE PER LITTER
C   BASED ON:
C LD         = DAY OF LACTATION (1-30)
C ADFMASS    = MASS OF ADULT FEMALES (KG)
C LITSIZ     = LITTER SIZE
C MLKENER    = ENERGY IN MILK (KJ/KG^.75*DAY) ESTIMATED
C                   FROM DATA OF MARTINET & DEMARNE (1984)
C LACT       = ENERGY IN MILK (KJ/KG*DAY)
C LACTEFF    = EFFICIENCY OF MILK PRODUCTION (A FRACTION)
C
C OUTPUT:
C LACTEN     = ENERGY OF LACTATION (KJ/KG*DAY) PER LITTER
C    MILK    = ENERGY IN MILK (kJ/KG*DAY) PER LITTER
C------------------------------------------------------------------
         MLKENER = 44.9818 + 8.6958*LD - 0.2529*(LD**2.0)
            LACT = MLKENER*(ADFMASS**0.75)/ADFMASS
            MILK = LACT*LITSIZ
          LACTEN = MILK/LACTEFF
         END
```

GORDON L. ROGOWITZ

CURRICULUM VITAE

EDUCATION

Ph.D. 1988	Department of Fisheries and Wildlife, Utah State University. Dissertation: A model of energy expenditure in white-tailed jackrabbits (*Lepus townsendii*) based on integrated studies of energetics and field ecology.
M.S. 1981	Department of Biology, State University of New York, Fredonia. Thesis: Habitat and food preferences of snowshoe hare (*Lepus americanus*) in western New York.
B.A. 1975	Department of Biology, Boston University.

RESEARCH EXPERIENCE

1982	Colorado Division of Wildlife, Fort Collins, CO. Cold-water fisheries, literature review.
1980-82	Department of Biology, Arizona State University, Tempe, AZ, under contract with U.S. Bureau of Reclamation. Habitats of mammals and birds in the Pecos River Valley, NM.
1977-78	Department of Anesthesiology, Harvard Medical School and Peter Bent Brigham Hospital, Boston, MA, with ARIEM, Natick, MA. Acclimation of mammalian pulmonary ventilation to high altitude.
1975-77	Department of Pharmacology, Boston University School of Medicine, Boston, MA. Growth and behavioral effects of morphine dependency.
1974	Department of Biology, Boston University, Boston, MA. Time-energy budgets of insectivorous bats (*Myotis lucifugus* and *Eptesicus fuscus*).

TEACHING EXPERIENCE

1983-84	Department of Fisheries and Wildlife, Utah State University. Teaching assistant: Sampling and Data Analysis for Biological Populations, Wildlife Techniques, Habitat Management.
1978-80	Department of Biology, State University of New York, Fredonia. Teaching assistant: General Biology, General Zoology.

GRANTS AND AWARDS

1985-88	Rob and Bessie Welder Wildlife Foundation, Fellowship. Approximately $10,000 per year.
1979	Sigma Xi Society, Grant-in-Aid of Research. $500
1974	National Science Foundation, URPP. Summer stipend.

PROFESSIONAL MEMBERSHIP

American Association for the Advancement of Science; American Institute of Biological Sciences; American Society of Mammalogists; Ecological Society of America; International Association for Ecology; The Wildlife Society

PUBLICATIONS

Rogowitz, G. L. 1988. Forage quality and use of reforested habitats by snowshoe hares. Can. J. Zool. 66:2080-2083.

Rogowitz, G. L. 1988. Measurement of simultaneous effects of air temperature, wind speed and short-wave irradiance on animal metabolism: a wind tunnel design. J. Physics E: Sci. Instrum. 21:903-904.

Rogowitz, G. L. 1988. Herbivory by snowshoe hares in reforested habitat. Saeugetierk. Mitt. 36. In Press.

ABSTRACTS

Rogowitz, G. L. 1985. The bioenergetics of white-tailed jackrabbits. Welder Wildlife Foundation Biennial Symposium, 1984-1985, Welder Wildlife Foundation, Sinton, TX.

Rogowitz, G. L. 1985. Evaluating snowshoe hare herbivory in conifer plantations. Fourth International Theriological Congress, August 13-20, University of Edmonton, Alberta, Canada.

Rogowitz, G. L. 1987. Combined effects of temperature, wind and thermal radiation on the metabolic rate of white-tailed jackrabbits, *Lepus townsendii*. American Society of Mammalogists, 67th Annual Meeting, June 21-25, 1987, University of New Mexico, Albuquerque, New Mexico.

Rogowitz, G. L. 1987. Thermoregulation in white-tailed jackrabbits (*Lepus townsendii*). Welder Wildlife Foundation Biennial Symposium, 1986-1987, Welder Wildlife Foundation, Sinton, TX.