DIET SELECTION, ACTIVITY PATTERNS AND BIOENERGETICS OF BIGHORN EWES IN CENTRAL IDAHO

Presented in Partial Fulfillment of the Requirements for the
Degree of Doctor of Philosophy
with a
Major in Forestry, Wildlife, and Range Sciences
in the
College of Graduate Studies
University of Idaho

by

Guy D. Wagner

May, 2000

Major Professor: James M. Peek, Ph.D.

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AUTHORIZATION TO SUBMIT

DISSERTATION

This dissertation of Guy D. Wagner, submitted for the degree of Doctor of Philosophy with a major in Forestry, Wildlife, and Range Sciences and titled "Diet selection, activity patterns, and bioenergetics of bighorn ewes in central Idaho" has been reviewed in final form, as indicated by the signatures and dates given below. Permission is now granted to submit final copies to the College of Graduate Studies for approval.

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Abstract

Knowledge of diet composition was necessary to assess the nutritional status of Rocky Mountain bighorn sheep in central Idaho. The objective was to determine and interpret the seasonal diet selection of the non-migratory portion of the population. Microhistological analysis of composite fecal samples was used to determine diet composition, and plant samples were analyzed for crude protein, digestibility, and macro and micro nutrients to examine forage quality. Graminoids constituted the majority of the diet throughout the year. However, forbs and browse provided important sources of nutrients at critical times of the year when grasses were low in nutritional value and digestibility. Non-migratory bighorns had developed flexible and dynamic feeding behaviors that allowed them to meet their nutritional needs while remaining in a relatively warm, dry environment.

Changes in bighorn ewe activity patterns were observed in response to season, forage quality, and weather. Ewes were equipped with motion-sensitive collars and monitored by automated remote telemetry and direct observation from 1994-1997. Bighorn ewes reduced activity during winter when forage resources were of low quality, and increased activity during spring and early summer. Ewes were most active during daylight hours, but during mid- and late-winter nocturnal activity increased. Within days, activity patterns were strongly bimodal during mid-winter, but exhibited several activity peaks during seasons with greater day-length. Ewes increased activity levels during the third trimester of gestation and while lactating. During this period of nutritional stress, they moved frequently while seeking high quality grasses and forbs.

The energy requirements and intake of bighorn ewes in central Idaho were unknown. Seasonal factorial models were constructed to assess the energy balance. Bighorn ewes met their energy requirements, except during winter days when they were inactive and failed to forage sufficiently to offset minimum energy requirements. Snow conditions, rather than extremes of temperature, profoundly influenced energy intake during winter. Models were sensitive to estimates of species specific bite rates and bite sizes. Poor forage quality in combination with deep or crusted snow may force bighorn ewes to operate at a negative energy balance.

Acknowledgments

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At Taylor Ranch, Jeff Yeo and Jette Morache always made us feel welcome, and provided many hours of interesting conversation. I thank Jeff especially for helpful insights during the early stages of field work. Also in the backcountry, ranch managers, Dave Duncan and Gary MacCalister, helped considerably with the field work and firewood cutting. Technicians, Aaron Foster and Scott Schrieber, collected data above and beyond the call of duty. The Idaho Dept. of Fish and Game were instrumental in capturing and collaring the bighorn ewes, especially Brian Holbrook, Mike Schlagel, and Dave Hunter. Dave Vales taught me how to run the remote telemetry units and provided many details that helped me get things up and running.

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Finally, I would like to thank my wife Teri whose love, hard work, and sacrifice enabled me to study wildlife biology. Her strength, perseverance, and companionship inspired me to keep striving through the roughest of times.

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Chapter 1

Introduction

Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) were widely distributed in western North America prior to the arrival of Europeans, and were estimated to number from 1.5 to 2 million (Buechner 1960). During the late 1800's and early 1900's bighorn sheep suffered severe population reductions across most of their range (Buechner 1960). Overhunting, competition for forage from domestic livestock, and diseases introduced via domestic livestock have been postulated as the causes of bighorn sheep population declines (Goodson 1982). In modern times, bighorn sheep numbers across North America have been estimated at less than 42,000 individuals (Wishart 1978), or less than 10% of their former levels (Buechner 1960).

In the Northern Rockies, bighorn sheep management has generally offered biologists more challenges than the management of other native ungulates (Cook 1990). Protection, through relatively strict hunting regulations, has generally failed to recover populations with the same degree of success witnessed in the cervidae. Reintroductions have been successful in some instances (Goodson 1982), but in other situations populations have continued to decline. Bighorn sheep populations have suffered from a general loss of habitat and more recent disease outbreaks (Risenhoover et al. 1988).

Bighorn sheep have specific habitat requirements and the amount of suitable habitat is limited. Many bighorn sheep populations have become small and isolated in remote areas (Trefethen 1975, Wishart 1978, Thorne et al. 1984). Berger (1990) concluded that populations of less than 50 individuals were likely to go extinct in less than 50 years. Bighorn sheep habitat can be characterized by three major components: high visibility, escape terrain, and abundant continuous forage (Risenhoover and Bailey 1985, Risenhoover et al. 1988). Suitable habitat areas often exist in discrete patches separated from one another. Furthermore, relative to other native ungulates, bighorn sheep are characterized by a reduced tendency to disperse (Geist 1971, 1983). Juvenile bighorn sheep inherit seasonal home ranges by following adults, and movement patterns are passed from one generation to the next. Individuals typically exhibit a strong fidelity to each seasonal home range (Geist 1971). Man-caused landscape disturbances and disease-related die-offs may sever traditional movement patterns. Consequently, bighorn sheep populations may become sedentary and fail to fully utilize available habitat. Thus, populations may not meet their nutritional needs or other environmental challenges (Douglas and Leslie 1999).

Bighorn sheep appear to be more susceptible to diseases than other native ruminants, and disease has played a greater role in bighorn sheep population ecology (Stelfox 1976, Geist 1985). Bighorn sheep evolved in cold climates where the number of pathogenic organisms were relatively low, and where bighorn sheep herds were segregated from closely related ruminant species (Geist 1985). Apparently, the spatial separation prevented bighorn sheep from co-evolving with a wide range of diseases. Consequently, bighorn sheep populations have recently encountered new pathogens introduced with domestic sheep to which they have little resistance.

Although most biologists accept food as the ultimate limiting factor of bighorn sheep populations, it is unclear what factors are actually regulating bighorn sheep populations (Dunbar 1992). Limiting factors determine the greatest absolute numbers that a population may obtain in a habitat. However, a population may be regulated by other density-dependent factors below the level set by limiting factors. Limited amounts of quality habitat and poor dispersal tendencies may accentuate density-dependent regulation through limited food resources (Cook 1990). One hypothesis suggests that declining nutritional status in bighorn sheep predisposes them to disease (Stelfox 1976, Schwantje 1986, Festa-Bianchet 1988a, 1988b, Cook 1990). In this model, limited food resources are the ultimate factors controlling populations, and diseases are the proximate cause of death.

An alternative hypothesis is that disease susceptibility is independent of nutrition. Bailey (1986), in the case of an all-age die-off in Colorado, concluded that dead bighorns were in excellent physical condition; indicating no shortage of forage. Ryder et al. (1992) concluded range conditions were good prior to a die-off of 40% of a bighorn herd in Wyoming. The possibility of virulent density-independent pathogens infusing from outside reservoirs (i. e. domestic livestock) cannot be dismissed (Foreyt and Jessup 1982, Wehausen et al. 1987, Onderka and Wishart 1988, Onderka et al. 1988, Foreyt 1989, Foreyt et al. 1994). Miller et al. (1991) concluded that pneumonia epizootics could be produced through density-independent and/or density-dependent mechanisms. Population density may increase to a certain threshold level where disease or a combination of factors may begin to regulate bighorn populations.

Risenhoover et al. (1988 p.346) state "that unless management priorities are adjusted to focus more closely upon the ecological requirements of bighorn sheep, surviving bighorn populations will remain predisposed to epizootics and land use conflicts, and additional sheep populations will be lost". The energy requirements of free-ranging bighorn sheep in central Idaho were unknown. The bioenergetics of bighorn sheep have been relatively little studied compared to the cervidae (Shackleton et al. 1999). The lack of adequate energy intake may have limited other northern ungulate populations (Parker et al. 1999).

Bighorn sheep must obtain sufficient energy from the forage they consume to survive and reproduce. The objectives of the this study were to: 1) determine seasonal diet composition and nutrient value, 2) develop activity and time budgets, 3) determine seasonal energy requirements and intakes, and 4) assess the seasonal energy balance of a subpopulation of bighorn ewes in central Idaho. To meet study objectives I chose a modeling approach.

Eberhart and Thomas (1991) recognize that field studies and environmental research often do not meet the criteria for modern experimental design, and that a more flexible approach may be more realistic in many outdoor situations. Eberhardt and Thomas (1991) distinguish between conducting a controlled experiment and observing an uncontrolled process by sampling. Inferences gained from controlled experiments are stronger, but in a wilderness context field-study objectives may be more realistically met by utilizing sampling procedures. One such procedure is "sampling for modeling" which provides efficient designs for estimating parameters in a specified model (Eberhardt 1978, Box and Lucas 1959). Modeling also efficiently combines the findings of many studies that address singular aspects into a functioning whole that places the reductionist studies in their ecological context (Hobbs 1989). Models should be objective-driven, and several "small" focused models are preferable to a single large complex model (Starfield 1997).

Nutritional studies of free-ranging wildlife require thorough knowledge of seasonal diet selection and nutritional content of forage resources. Chapter 2 reports the seasonal diet of bighorn sheep residing in the study area as determined by microhistological fecal analysis.

Activity is one of the major energy expenditures of wild animals, and knowledge of time budgets is necessary for understanding their bioenergetics. Chapter 3 reports the activity patterns and time budgets of bighorn ewes as recorded by remote radio-telemetry and direct observation.

In Chapter 4, data from Chapters 2 and 3, along with values obtained from the literature, were combined into a series of models that calculated the energy requirements and energy intake of resident bighorn ewes. Values were calculated for each of 5 seasons or periods to reflect seasonal changes in plant phenology and bighorn sheep physiology.

Sexual segregation in bighorn sheep habitat use required considering male and female segments of the population independently (Jorgenson et al. 1993). Population characteristics of the female segment most likely influenced long-term trends in the overall population more so than did the male segment. Consequently, research efforts emphasized the female cohort.

History of Bighorn Herd in Big Creek, Idaho

Bighorn sheep have probably occupied the Big Creek and Middle Fork drainages of central Idaho since the late Pleistocene. Bighorn sheep formed an important component of native American culture in the area, and the first Europeans to enter the drainage reported bighorn sheep in the thousands (Smith 1951, 1954). The bighorn sheep herds inhabiting the Big Creek and Middle Fork drainages of central Idaho apparently experienced a severe decline following European settlement of the area (Smith 1951, 1954). Overhunting and diseases introduced with domestic livestock were apparently responsible for the decline. Between 1870 and 1880 many sheep died from what appeared to be scabies, caused by Psoroptes spp. mites (Smith 1951, 1954; Goodson 1982). Another severe die-off occurred around 1910. Bighorn sheep populations apparently never recovered to pre-European levels.

For approximately the last half-century, bighorn sheep herds in the area have experienced only limited hunting for trophy rams. The female component of the population has not been hunted regularly for decades, and they have basically been left to fluctuate within a habitat relatively little affected by modern man. However, limited market hunting may have occurred during the 1910-1920 period (J. Peek pers. commun.). Since the 1930's, numbers of permanent human residents and livestock have steadily declined under wilderness management. Bighorn sheep populations in the Big Creek and Middle Fork drainages have presented the opportunity to study the relationship between a wild ungulate and its environment in a relatively intact ecosystem.

Akenson (1992) studied the interspecific competition of bighorn sheep, mule deer (Odocoileus hemionus), and elk (Cervus elaphus) on the Big Creek winter range. Bighorn sheep and mule deer showed a positive spatial affiliation. Mule deer were not considered to be important competitors of bighorn sheep for winter forage, because of species specific differences in diet selection. Elk and bighorn sheep did not show a positive spatial affiliation. Low use of the study area by elk during the duration of the study made it difficult to assess this relationship. Elk numbers have continued to increase in the Big Creek drainage, and the potential for competition exists between elk and bighorn sheep during severe winters.

Bighorn sheep populations have suffered several declines over the years, but bighorn populations increased to record high numbers in recent times during the late 1980's. However, in 1986, lamb:ewe ratios fell from 35-45 lambs per 100 ewes to <16 lambs per 100 ewes, and ratios remained at this level through 1991. By 1991, the overall population had experienced a sharp decline (Akenson and Akenson 1992).

Akenson and Akenson (1992) studied movement patterns of ewes captured on the Cliff Creek (a tributary of Big Creek) winter range. Previous to this study only the low elevation lambing area on Cliff Creek had been known. Radio-tracking revealed that a number of ewes migrated to lambing areas in other drainages. Some of these areas were at higher elevations in Monumental, Big Cottonwood, and Dynamite Creeks, up to 40 km from the Cliff Creek winter range. Tissue samples collected from dead ewes ($\underline{n}$ = 3) and lambs ($\underline{n}$ = 7), revealed the presence of several bacterial pathogens including Pasteurella trehalosi and P. multocida (Hunter 1990).

Akenson and Akenson (1992) concluded their study in 1990, and monitoring has consisted of periodic aerial counts conducted by the Idaho Fish and Game Department. Akenson and Akenson (1992) postulated that the bighorn sheep populations were possibly stressed by competition with elk, severe spring weather, or extended drought conditions in the 1980's. Predation was not considered to be an important mortality factor.

Study Area Description

The study was conducted within the Big Creek drainage of central Idaho (Figure 1.1), and the Taylor Ranch Field Station of the University of Idaho Wilderness Research Center served as the base of operations. Big Creek flows from west to east and is a major tributary of the Middle Fork of the Salmon River. Big Creek is located within the 2.3 million acre Frank Church River of No Return Wilderness. Elevations within the drainage range from 1067 m to 2896 m, and contain some of the greatest relief in Idaho. Lower elevations are characterized by steep V-shaped canyons. Higher elevations contain alpine basins, forested ridge tops, and meadows. Abrupt changes in aspect result in markedly different plant associations.

Southern exposures at lower elevations, where soil development is adequate, are generally dominated by grasslands. The major soil type on southern exposures is brown podzol (Ross and Savage 1967, Tisdale et al. 1969, Claar 1973). Soils are formed from granitic Idaho batholith parent material (Claar 1973), and are generally shallow and rocky. Numerous rock outcrops, cliffs, and talus slopes are present. Bluebunch wheatgrass (Pseudoroegnenia spicata), Idaho fescue (Festuca idahoensis), junegrass (Koeleria cristata), needle and thread grass (Hesperochloa comata), Sandberg's bluegrass (Poa sandbergii), onion grass (Melica bulbosa), and cheat grass (Bromus tectorum) comprise the majority of graminoid biomass. Big sagebrush (Artemesia tridentata), rabbitbrush (Erecaneria nauseose), and bitterbrush (Purshia tridentata) are important shrub species associated with grasslands. Mountain mahogany (Cercocarpus ledifolius) forms extensive stands on steep rocky outcrops. Wax current (Ribes cereum), Gooding's gooseberry (R. velutinum), Oregon grape (Berberis repens), chokecherry (Prunus virginiana), and serviceberry (Amelanchier alnifolia) are also frequently encountered shrubs. Arrow-leaf balsamroot (Balsamorhiza sagittata), western yarrow (Achillea millefolium), and lupine (Lupinus spp.) are important forbs. Along streams, Douglas-fir (Pseudotsuga menziesii), aspen (Populus tremuloides), black cottonwood (Populus trichocarpa), red-osier dogwood (Cornus stolonifera), hawthorn (Crataegus douglasii), willow (Salix spp.), and thimbleberry (Rubus parviflorus) constitute major species. Southern exposures comprise the majority of the terrain on the north side of Big Creek. This area serves as important winter range for bighorn sheep, mule deer, and elk. Snow depths are generally low and southern aspects usually remain snow-free for much of the winter. The winter range extends for 48 km along the lower portion of the drainage.

Douglas-fir forests are encountered on north aspects and ridgetops. Small stands and individual Douglas-fir are also scattered throughout the grasslands. On north aspects understory plants include ninebark (Physocarpus malvaceus), shinyleaf spirea (Spiraea betulifolia), snowberry (Symphoricarpus alba), rose (Rosa spp.), mountain maple (Acer glabrum), and serviceberry. Pinegrass (Calamagrostis rubescens) and elk sedge (Carex geyeri) are important graminoids. All plant names follow the National Plant Data Base, U. S. Dept. of Agriculture (http://plants.usda.gov/plants).

In addition to bighorn sheep, mule deer, and elk, other native ungulates include small populations of moose (Alces alces), white-tailed deer (Odocoileus virginianus), and mountain goats (Oreamnos americanus). Potential predators of bighorn sheep inhabiting the area include mountain lions (Felis concolor), bobcats (F. rufus), black bears (Ursus americanus), gray wolves (Canis lupus), coyotes (Canis latrans), and golden eagles (Aquila chrysaetos).

Numbers of native ungulates have changed since the turn of the century. Few elk were living in the Middle Fork of the Salmon region during the early 1900's (Smith 1954). Elk numbers have increased steadily since the 1940's (Hornocker 1970), and Idaho Dept. of Fish and Game aerial counts from 1973 to 1989 indicate that elk numbers on Big Creek have increased dramatically in recent years (Akenson 1992). Mule deer populations have fluctuated markedly over time, reaching peak numbers during the 1940's and 1950's. Current mule deer populations appear to be lower than 10 years ago.

Summers were typically hot and dry with July and August usually having the highest average temperatures (Figures 1.2 - 1.5). Typically, maximum daily July temperatures averaged 35 C. Temperature patterns were relatively consistent from year to year. However, September 1994 was unusually warm and dry, and produced average daily temperatures higher than August's (Figure 1.2). Moisture patterns were more variable than temperature patterns (Figures 1.6 - 1.9). Total annual precipitation was 31.3, 53.8, 39.4, and 43.1 cm during 1994 - 1997 (National Weather Service, respectively). Over the long-term, annual precipitation has averaged 38.1 cm at Taylor Ranch in Big Creek. August and September were typically the months receiving the least precipitation. The remainder of annual precipitation occurred during winter in the form of snow or spring rain. Winter snowfall varied substantially between years. Snowfall during the months November - February was 37.3 cm during the winter of 1994-95, 93.7 cm during the winter of 1995-96, and 84.8 cm during the winter of 1996-97 (National Weather Service).

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Figure 1.1 Study area map of Big Creek, Idaho
a tributary of the Middle Fork of the Salmon River
Frank Church River of No Return Wilderness

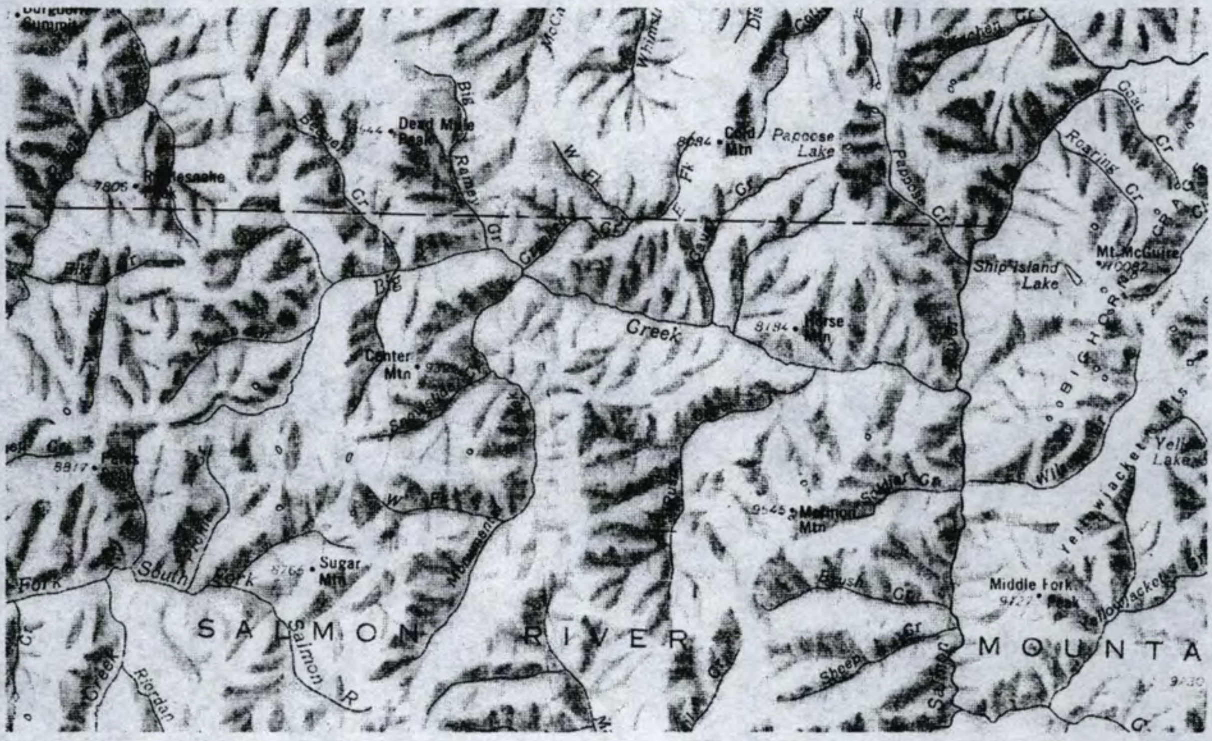
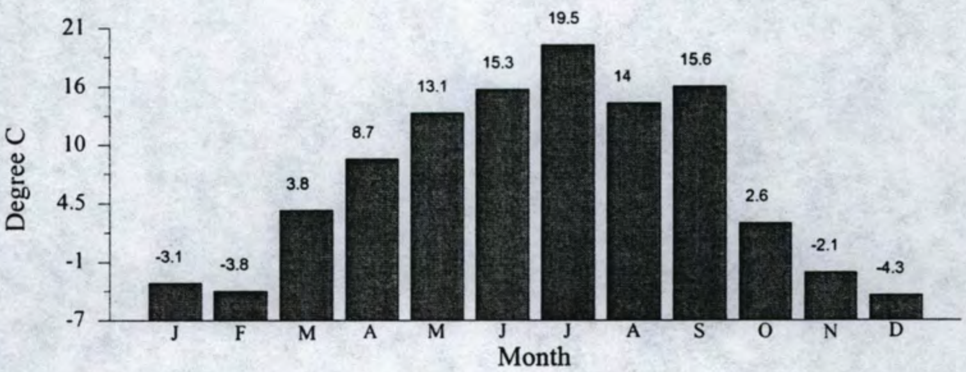


Figure 1.2 Average monthly temperature 1994



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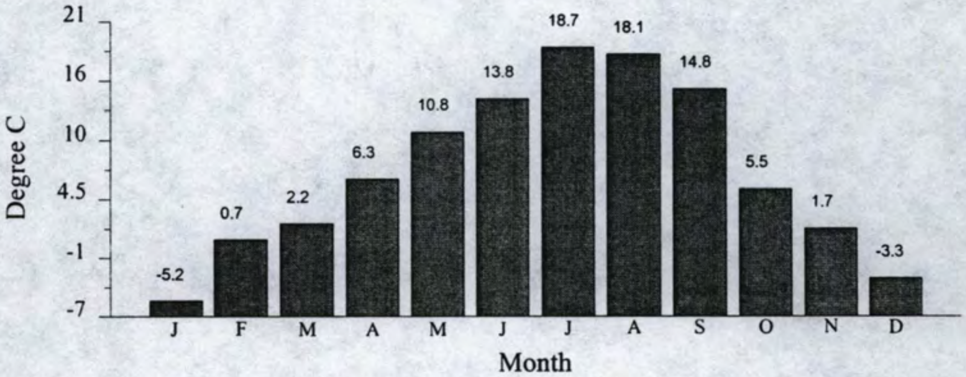

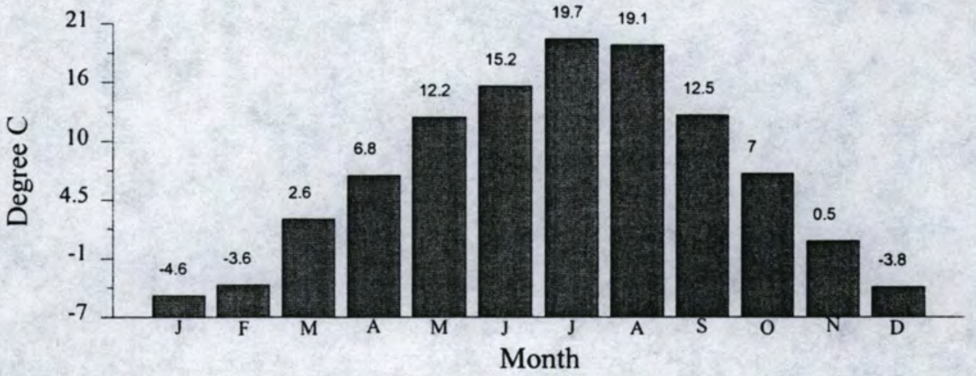

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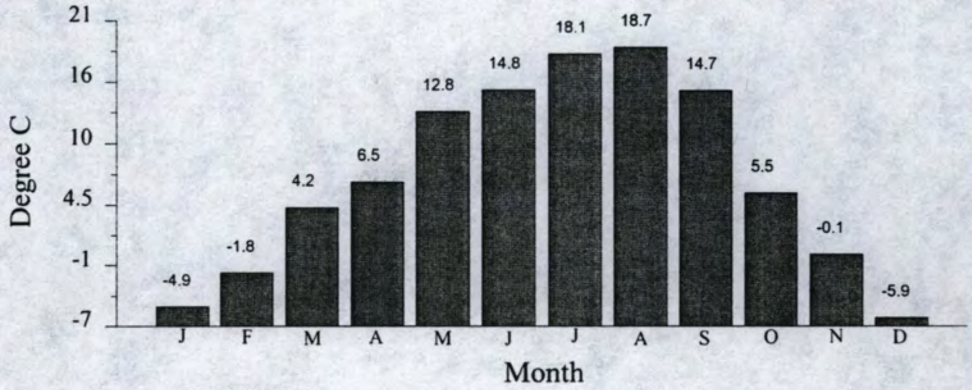


Figure 1.5 Average monthly temperature 1997

Figure 1.6 Total monthly precipitation 1994

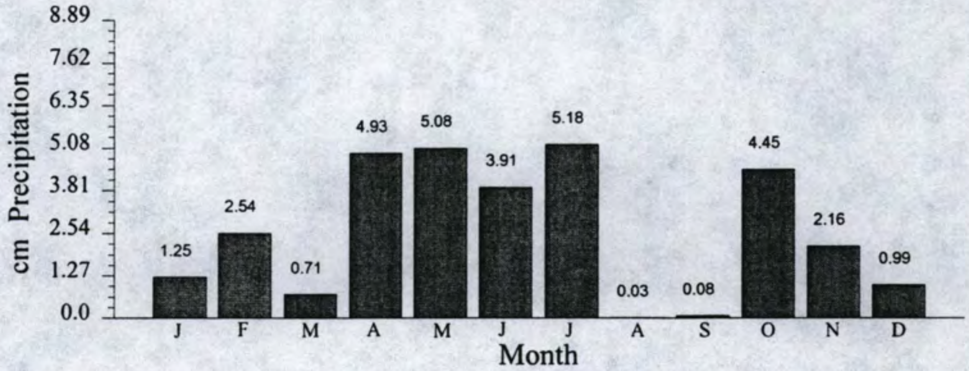


Figure 1.7 Total monthly precipitation 1995

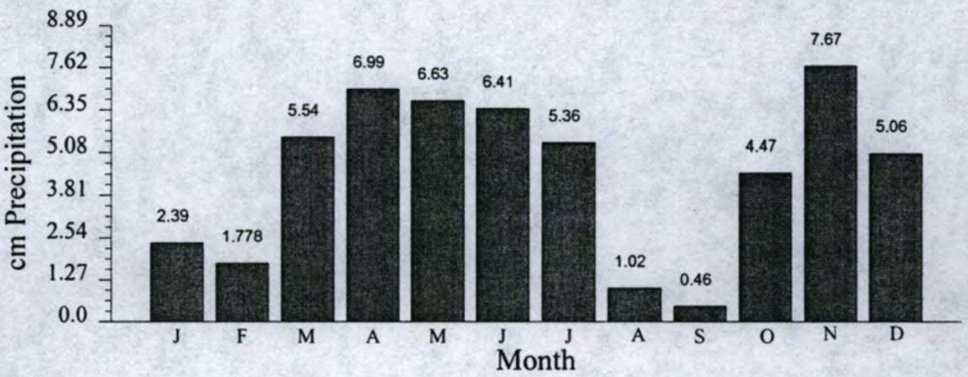


Figure 1.8 Total monthly precipitation 1996

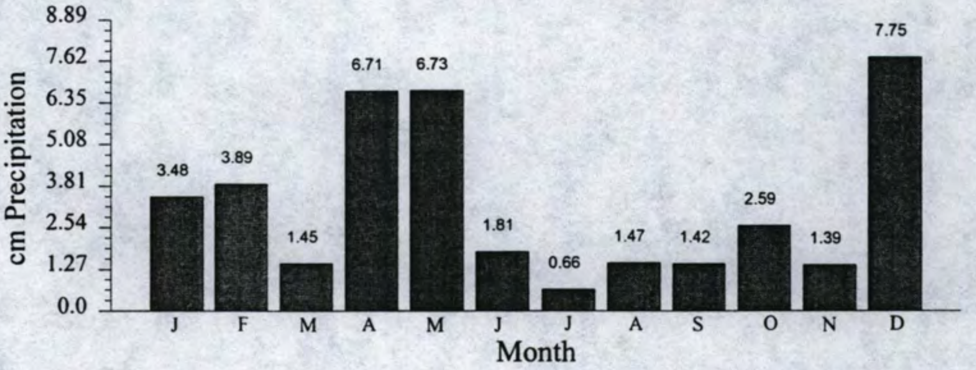
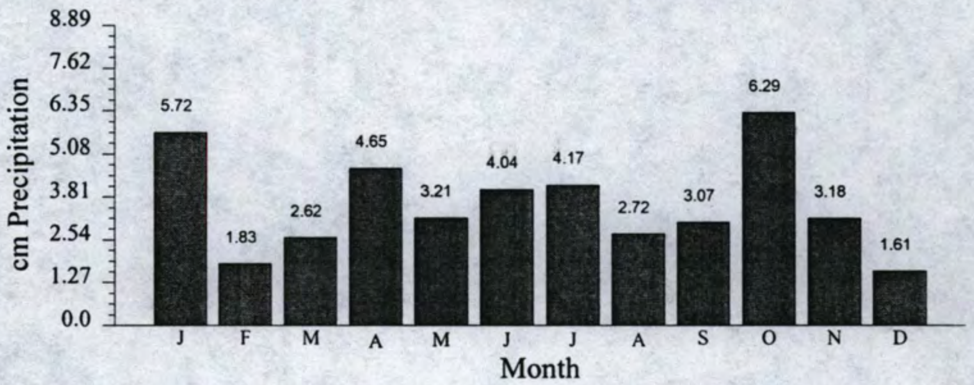


Figure 1.9 Total monthly precipitation 1997



Chapter 2

Bighorn Sheep Diet Selection in Central Idaho

INTRODUCTION

Bighorn sheep (Ovis canadensis canadensis) inhabiting the Big Creek drainage of central Idaho have experienced population fluctuations characterized by rapid declines from high numbers, that were followed by extended periods of low recruitment. Population declines were associated with the presence of several pneumonia-causing pathogens including Pasteurella trehalosi and P. multocida (Hunter 1990, Jaworski 1993). However, it was unclear whether disease alone caused population die-offs or whether a combination of interacting factors, such as competition, severe weather, and poor nutrition, combined to lower disease resistance. Obtaining a thorough knowledge of local bighorn diet was a prerequisite for assessing the nutritional status of bighorn sheep in the area, and for interpreting observed behaviors.

Bighorns evolved massive jaws, large molar teeth, and comparatively large rumens and omasums. Consequently, bighorns have been regarded as specialized grazing animals adapted to a diet of coarse graminoid vegetation (Geist 1971). However, bighorns at some locations and life stages have consumed appreciable amounts of browse and forbs. In Colorado, summer diet of adult bighorn sheep consisted of 73-94% leaves of woody plants, mainly true mountain mahogany (Cercocarpus montanus, Rominger et al. 1988). Winter diet studies indicated that the percentages of grasses, shrubs, and forbs varied widely between populations. Winter diets from Thompson Falls (Tilton and Willard 1981) and Sun River

(Schallenberger 1965), Montana were highest in shrubs. While, diet studies conducted in British Columbia (Blood 1967), northcentral Montana (Kasworm et al.1984), and Yellowstone National Park (Oldemeyer et al. 1971, Keating 1985) reported winter diets were highest in graminoids. Hobbs et al. (1983) reported bighorn lambs selected a diet dominated by forbs, but later determined that adult diet conformed to previously held beliefs that bighorn sheep were primarily grazers (Baker and Hobbs 1987).

Studies that followed bighorn sheep diet throughout the year concluded that a variety of grasses, forbs, and shrubs were important at different times of the year. Wikeem and Pitt (1992, p 334) followed the diet of California bighorn sheep (Ovis canadensis californiana) in British Columbia continuously for 2 years, and concluded that "quality habitat depends more on a complement of plant species, which provides a diversity of forage alternatives, than on dominance by a few, albeit key management species". Desert bighorn sheep (O. c. mexicana) in Arizona similarly used a wide variety of forage species throughout the year (Miller and Gaud 1989). The unpredictable nature of the desert environment required bighorn sheep to adjust their diet as the vegetation changed.

Within the greater Big Creek population a substantial number of bighorn ewes migrated over 40 km from low elevation winter range to high elevation summer ranges. Migratory ewes gained over 1829 m in elevation (Akenson and Akenson 1992). However, other ewes did not actually migrate, and could be located within the same area all year. At most, they frequented slightly higher elevations during late summer and early fall. However, they descended to Big Creek for water throughout the year, and consequently could be located at low elevations during all seasons.

Hebert (1973) demonstrated with captive bighorns that high elevation summer forages were more nutritious than forages typically consumed on winter ranges. Bighorn sheep that consumed high-elevation forages during the summer entered the winter in better condition, were more efficient at utilizing winter range forages, and responded physiologically faster to spring green-up than sedentary bighorns maintained on winter range forages year-round. Essentially, the "alpine" bighorns extended the period of spring green-up and its nutritious forage for months, while the "sedentary" bighorns encountered winter forage conditions months earlier.

The objective of this study was to determine and interpret the seasonal diet selection of the non-migratory portion of the population. We believed the "sedentary" ewes had developed flexible and dynamic feeding behaviors that allowed them to meet their nutritional needs while remaining in a relatively warm, dry environment.

STUDY AREA

Big Creek flows predominantly west to east and drains into the Middle Fork of the Salmon River. Elevations within the drainage range from 1067 to 2896 m, and contain some of the greatest relief in Idaho. Southern exposures comprise the majority of the terrain on the north side of Big Creek. This area serves as important winter range to bighorn sheep, mule deer (Odocoileus hemionus), and elk (Cervus elaphus). Snow depths are generally low and southern aspects usually remain snow-free for much of the winter. The greater winter range extends for 48 km along the lower portion of the drainage. However, bighorn sheep occupy mainly the lower 19 km of the winter range.

Topography at lower elevations is characterized by steep V-shaped canyons. Abrupt changes in aspect result in markedly different plant associations. Southern exposures at lower elevations, where soil development is adequate, are dominated by grasslands. Soils are formed from granitic Idaho batholith parent material (Claar 1973), and are generally shallow and rocky. Numerous rock outcrops, cliffs, and talus slopes are present.

Bluebunch wheatgrass (*Pseudoroegnenia spicata*), Idaho fescue (*Festuca idahoensis*), junegrass (*Koeleria cristata*), needle and thread grass (*Hesperochloa comata*), Sandberg's bluegrass (*Poa sandbergii*), and cheat grass (*Bromus tectorum*) comprise the majority of graminoid biomass. Big sagebrush (*Artemesia tridentata*), rabbitbrush (*Erecaneria nauseose*), and bitterbrush (*Purshia tridentata*) are important shrub species associated with grasslands. Curl-leaf mountain mahogany (*Cercocarpus ledifolius*) forms extensive stands on steep rocky outcrops. Arrowleaf balsamroot (*Balsamorhiza sagittata*), Western yarrow (*Achillea millefolium*), and lupine (*Lupinus* spp.) are important forbs. Douglas-fir forests are encountered on north aspects and ridgetops. Small stands and individual Douglas-fir are also scattered throughout the grasslands. All plant names follow the National Plant Data Base, U. S. Dept. of Agriculture (http://plants.usda.gov).

Summers were typically hot and dry, with July and August usually having the highest average temperatures. Typically, maximum daily July temperatures averaged 35 C. Temperature patterns were relatively consistent from year to year. However, September 1994 was unusually warm and dry, and produced average daily temperatures higher than August's. Moisture patterns were more variable than temperature patterns. Total annual precipitation was 31.3, 53.8, 39.4, and 43.1 cm during 1994 - 1997 (National Weather Service, respectively). Over the long-term, annual precipitation has averaged 38.1 cm at Taylor Ranch in Big Creek. August and September were typically the months receiving the least precipitation. The remainder of annual precipitation occurred during winter in the form of snow or as spring rain. Winter snowfall varied substantially between years. Snowfall from November - February totaled 37.3 cm during the winter of 1994-95, 93.7 cm during 1995-96, and 84.8 cm during 1996-97.

METHODS

Diet Composition

Diet composition may be determined by 5 methods: rumen analysis, fecal analysis, esophageal fistula, direct observation, and feeding site surveys (Litvaitis et al. 1994). Rumen analysis requires killing the study animal, or capture and implantation of a rumen fistula. Neither of these options or the implantation of esophageal fistulas were practical methods for wild bighorn sheep in the study area. Hunting was restricted to only the older male segment of the population (6 permits/year), and the use of fistulas would have required recapturing bighorns at short intervals. Direct observation was occasionally possible, and was attempted throughout the duration of the study. However, this method required a relatively close observer-animal distance, vegetative conditions that allowed accurate identification of plant species consumed, plus ideal topography, lighting, and weather conditions. These factors seldom occurred simultaneously for a sufficient time period to reliably estimate diet composition. Feeding site surveys were difficult to conduct, because sheep, as well as elk and mule deer, repeatedly fed across the same areas. Thus, informal feeding site examinations were conducted to obtain a general knowledge of the plant species being utilized.

Fecal analysis represented the best method for obtaining an estimate of diet composition for free-ranging bighorn sheep (Todd and Hansen 1973, McInnis et al. 1983, McInnis and Vavra 1987). Wikeem and Pitt (1992) considered fecal analysis the only practical method for determining the diet of free-ranging herbivores, even though their study was conducted within a 42 ha enclosure. The use of microhistological fecal analysis enabled researchers to follow the seasonal diet selection of a group of animals through time without eliminating individuals. Also, in most situations larger sample sizes were easier to collect compared to rumen samples.

The results of fecal analysis may be influenced by differential digestibilities. Highly digestible items may not be identifiable in fecal samples, and other items may be modified by the digestion process making a fine resolution of identification impractical. The method also requires a high degree of skill and lengthy training. However, when tested the method has produced acceptable results with bighorn sheep diets (Todd and Hansen 1973).

Mule deer shared winter and summer ranges with bighorns. Therefore, pellets were collected from directly observed bighorn sheep. From late fall to early spring mature rams accompanied ewes, and several immature rams remained with ewe bands through the summer months. Consequently, fecal samples contained pellets from both sexes, although the majority were from ewes. Very few lambs survived, and an insufficient number of "lamb-only" samples were obtained for analysis. Microbial decomposition of collected samples was prevented by adding an equal volume of table salt and air drying in paper bags (Hansen et al. 1978). A composite sample was collected each week by obtaining 6 pellets from 15 to 57 fecal piles. Samples were collected from June 1994 to February 1995, from January to August 1996, and from January to May 1997. Samples were analyzed at the Washington State University Wildlife Habitat Laboratory in Pullman, Wash. Each composite sample received 150 microscope views, from which the percent composition was calculated. Forage species were identified to the lowest taxon possible.

Forage Quality

Composite samples of forage species were collected for later nutritional analysis. Samples were collected from sites where bighorns frequently were observed feeding. A compass bearing was randomly generated on a hand-held calculator, and a portion of the nearest target species was collected every 5 meters, a minimum of 10 plants were sampled at each site. Each species was collected from 3 different sites at approximately 2 week intervals. Samples were placed in paper bags, air dried, shipped to the University of Idaho, and oven dried at 40 C for 48 hrs. Plant parts consumed by bighorn sheep were separated and ground with a Wiley mill to pass through a 1 mm screen. Only 1 bighorn sheep diet study (Smith 1954) had been conducted near the study area, therefore certain plant species were not known to be consumed by bighorn sheep until after the results of the microhistological fecal analysis became available.

Portions of composite samples were analyzed at the University of Idaho Analytical Sciences Laboratory in Moscow, Idaho for macro (Na, K, Ca, Mg, P, S) and micro (Cr, Co, Cu, Fe, Mn,, Zn) minerals, and total C, H, and N. A separate analysis for Se was conducted on a subset of composite samples for bluebunch wheatgrass, curl-leaf mountain mahogany, and bitterbrush. Crude protein was estimated by multiplying total N by 6.25 (Robbins 1993). Macro and micro minerals were analyzed by inductively coupled plasma optical emission spectroscopy (ICP). Selenium was analyzed in a similar procedure only the sample was first treated by acid digestion using nitric, perchloric, and sulfuric acids, followed by hydride generation before being subjected to ICP. Carbon, Hydrogen, and Nitrogen were analyzed by furnace combustion.

Apparent in vitro digestible dry matter (IVDDM) was determined using a modified version of the method developed by Tilley and Terry (1963). Forage samples of 0.25 g were placed in porous bags, heat sealed, and incubated in an Ankom Technology Daisy II 200/220 Rumen Fermenter for 48 hr at 39 C. Inoculum was obtained from 3 domestic beef cows maintained on a grass diet. Two replicate trials were conducted and the values averaged. The residue obtained after fermentation was a combination of undigested substrate and microbial cells (Van Soest 1982). Correction factors to subtract the microbial cell fraction adhering to bags were obtained by including blank porous bags within each batch of inoculum. Correction factors were applied by averaging dried weights of blanks and subtracting this value from sample weights.

Data Analysis

Based upon the annual reproductive cycle of bighorn ewes and plant phenology, a year was divided into 5 periods. Summer or Period 1 (1 June to 16 August) corresponded to peak lamb drop and lactation, and availability of early summer forage. Late summer-fall or Period 2 (17 August to 15 November) corresponded to decreased lactation, gradual senescence of most herbaceous forage, possible fall resprouting of some grass species, and beginning of winter weather. Winter or Period 3 (16 November to 15 February) corresponded to mid-winter conditions of frequent snowfall, relatively low temperatures, senescent forage, and mating. Late winter or Period 4 (15 February to 31 March) corresponded to approximately the second trimester of gestation, and earliest green-up of some grasses. Spring green-up or Period 5 (1 April to 31 May) corresponded to the third trimester of gestation, green-up of all forages, and eventually movement to lambing ranges.

Diet composition values for each forage species within a period were calculated by averaging individual fecal sample values. Only forage species comprising ≥ 1 % of at least 1 period were included in analyses. Forage species were also combined into grasses, forbs, browse, conifers, and mosses/lichens categories for each period. Differences between years for forage categories were tested by t-test or 1-way analysis of variance (ANOVA). Differences between periods for grasses, forbs, and browse forage categories were tested with a 1-way multivariate analysis of variance (MANOVA) and univariate ANOVA. Means were separated using Duncan's multiple range tests. Similar to Hobbs et al. (1981), percentages were treated as normally distributed, and were not arc-sine transformed. Transformation did not alter estimates of the variance beyond the third decimal place, and consequently did not affect the results of statistical tests. In addition, Butchner and Kemp (1974) found no difference in statistical power between analysis of variance using transformed and untransformed data. Where sample sizes differed, random subsampling was conducted to obtain balanced designs, because such designs were more robust to violations of the assumption of heterogeneity of variance (Kirk 1982). Period diets were compared for similarity with Spearman's rank correlation coefficient (ρ) and Renkonen percent similarity index (Krebs 1989). Period trends in diet composition were examined graphically, and period trends in crude protein, IVDDM, and macro and micro nutrients were analyzed by linear and polynomial regression. Models were chosen using a model selection criterion (Statmost User's Guide 1995) defined as:

$$MSC = \ln\left(\sum_{i=1}^{n}(y_i - \bar{y})^2 \div \sum_{i=1}^{n}(y_i - Y_i)^2\right) - \frac{2p}{n}$$

where *MSC* = model selection criterion, y = observed values, Y = predicted values, p = number of parameters, and n = sample size. The MSC represents the information content of a given set of parameter estimations by normalizing the coefficient of determination to the parameter number.

RESULTS

Diet Composition

There were no significant differences between years in percent of diet composition for forage categories except during winter. During winter, shrubs were significantly higher ($\underline{P}$ = 0.001) in percent composition in 1995-96 than in 1994-95 or 1996-97. Shrubs averaged 37.27% during 1995-96 compared to 3.04% and 10.45% in 1994-95 and 1996-97, respectively.

Percent diet composition of grasses, forbs, and browse differed between time periods. The null hypothesis of no overall period effect tested by MANOVA was rejected ($\underline{P}$ = 0.001, Wilks' Lambda). Univariate tests were significant ($\underline{P}$ = 0.001) for grasses, forbs, browse, conifers, and mosses/lichens. Partial correlation coefficients showed that grass consumption was inversely related to both forb and browse consumption (-0.84 and -0.68, respectively). When consumption of grasses increased to high levels, the consumption of other forage types declined.

Graminoids formed the largest component of the bighorn diet during all periods of the year (Figure 2.1). Bluebunch wheatgrass, cheatgrass, Idaho fescue, bluegrasses, and needle-and-thread grass were the most important graminoids in the diet. Bluebunch wheatgrass formed the largest single-species component of the diet at all periods of the year (Table 2.1, Figure 2.1). Idaho fescue, bluegrasses, and needle-and-thread grass were important during all periods of the year, but reached their peak during spring green-up. Highest consumption of grasses occurred during winter and spring green-up, and lowest consumption occurred during summer and late summer-fall (P = 0.001).

Forbs reached their peak in diet composition during summer and late summer-fall, corresponding with June through November (Figure 2.1). Significantly more forbs were consumed during these 2 periods than during winter, late winter, and spring green-up (P = 0.001). The most prominent species in the diet were western yarrow, Thelypodium sp., Astragalus sp., Cirisium sp., Erigeron sp., Eriogonum sp., Lesquerella sp., Lupinus sp., and Phacelia sp. (Table 2.1). As expected, during the remainder of the year forbs formed a much smaller proportion of the diet due to senescence. Arrowleaf balsamroot was a major exception, reaching peak levels in the diet during the winter months. Bighorn frequently pawed through snow to consume the semi-decomposed balsamroot leaves. Indeed, if not for the consumption of balsamroot, percent composition of forbs would have been several orders of magnitude lower during the winter months. Eriogonum sp. and Phacelia sp. were also forbs that persisted at appreciable levels in the diet during the winter months. Biscuitroot (Lomatium dissectum) was not identified in the microhistological fecal analysis. Nevertheless, during the winter bighorn sheep were often observed pawing up and consuming the tubers of this plant whenever the ground was not frozen. They also consumed the roots of arrowleaf balsamroot, and the tuber fragments of these species may have appeared identical under the microscope (Kasworm et al. 1984).

Browse was greatest in percent diet composition during summer (21.90%) and late summer-fall (18.40%; Figure 2.1). Then browse consumption declined in winter (14.9%), and late winter (12.17%), and fell to relatively low levels (3.86%) during spring green-up

(Table 2.1). Significantly more browse was consumed during summer, late summer-fall, and winter, than during spring green-up ($\underline{P} = 0.001$). However, the winter of 1995-96 was an exception; browse consumption was significantly higher (37.27%), and browse formed a larger portion of the diet. The major browse species consumed were mountain mahogany and bitterbrush (Table 2.1). However, ninebark, currants (Ribes sp.), and serviceberry were of importance during summer and late summer-fall, and willows (Salix sp.) were important during late winter. During late summer-fall, bighorn sheep were frequently observed feeding on elderberry (Sambucus cerulea). Although identified in the fecal analysis, this species did not reach ≥ 1 % composition in the diet.

Conifers, mainly Douglas-fir, appeared in the diet during winter (1.02%), late winter (7.32%) and spring green-up (3.15%,Table 2.1). Only twice during the entire study were bighorns observed actually browsing on Douglas-fir. However, Douglas-fir needles were sometimes mixed thoroughly with Idaho fescue on the ground. Therefore, some needles may have been consumed while sheep were grazing beneath trees during winter.

Spearman's rank correlation coefficients (ρ) showed that summer diet was correlated with other period diets except for late winter. Late summer-fall diet was only correlated with summer diet, and winter, late winter, and spring green-up diets were correlated with each other. Percent similarity indexes generally decreased in similarity the farther apart period diets were in time (Table 2.2).

Forage Quality

Protein content for grasses and forbs was high during summer, and declined throughout late summer-fall to their lowest levels by winter. By late-winter crude protein levels began slowly increasing, and then rapidly reached peak levels during spring green-up. Crude protein levels between grasses and forbs were not significantly different during spring green-up or summer, however, through late summer-fall, winter, and late winter forbs contained significantly more protein than grasses ($\underline{P} = 0.001$). Percent crude protein content for grasses and forbs were described by fourth and second order polynomial equations, respectively (Figures 2.2 and 2.3). In contrast, protein content of shrubs (Figure 2.4) did not demonstrate any significant relationship with period. Protein levels of shrubs remained approximately constant throughout all periods.

In vitro digestible dry matter of grasses decreased from summer to late summer-fall. In vitro digestible dry matter of grasses was described by a fourth order polynomial equation (Figure 2.5). Digestibility of grasses reached its lowest level during late winter, before rapidly increasing during spring green-up. For forbs, IVDDM did not show a significant relationship with period (Figure 2.6). However, IVDDM increased linearly from summer to spring green-up for shrubs (Figure 2.7).

Phosphorus, potassium, and sulfur content of grasses, forbs, and browse followed the same pattern exhibited by crude protein. Levels were high during summer, then declined steadily to low levels during winter, which were followed by rapid increases during spring green-up. All three nutrient concentrations for grasses, forbs, and browse were described by second or third order polynomial equations (Figures 2.8 - 2.16). Magnesium followed the above pattern for grasses and forbs (Figures 2.17 and 2.18), however no significant relationship existed for shrubs. Copper followed the same quadratic relationship for grasses and shrubs (Figures 2.19 and 2.20) , but no relationship existed for forbs. Zinc content of grasses (Figure 2.21) demonstrated a quadratic relationship, with highest content during summer and spring green-up. No relationship between zinc content and period was evident for forbs and shrubs.

Calcium content did not fluctuate through time for grasses and forbs, but maintained a roughly constant level. However, it increased during the winter for shrubs (Figure 2.22). Since phosphorous content followed the opposite pattern, the calcium-phosphorous ratio increased during late summer-fall and winter months for grasses and shrubs (Figures 2.23 and 2.24). Sodium content did not exhibit any significant trends through time for grasses, forbs or shrubs. Trends in iron content were erratic for all 3 forage categories. Very few samples from any forage category contained detectable levels of the trace minerals cobalt, chromium, and selenium.

DISCUSSION

Bighorn sheep inhabiting the lower elevations of the Big Creek drainage conform to Geist's (1971) assertion that bighorns are primarily grazing animals. However, at certain times of year forbs and shrubs make important contributions to the diet. Differences between period diets were largely explained by increases in forb and shrub consumption and decreases in grass consumption. Daily et al. (1984) and Wikeem and Pitt (1992) also reported high forb consumption during summer months, followed by reductions in consumption as forbs reached senescence.

Many individual forb species were much less common than grass species, such as bluebunch wheatgrass. Even though individual forbs constituted small percentages of the diet, definite preferences for some forb species can be inferred when their low relative availability is considered (Wikeem and Pitt 1992). In addition, forbs collectively furnished an important source of nutrients during peak lactation, and may have enabled bighorns to accumulate nutrient reserves prior to winter. During summer and late summer-fall the average crude protein content of forbs was higher than grasses, and certain individual forb species had much higher crude protein content than did grass species. For example, during late summer-fall Thelypodium sp. had an average crude protein content of 16.3%, while bluebunch wheatgrass averaged 4.8%. Yet, bluebunch wheatgrass composed 23.28% of the diet compared to the forb's 8.1% (Table 2.1). Furthermore, even though both forage categories were declining in protein content and other nutrients, forbs were not declining as rapidly as grasses. Thus, forbs may play an important role in allowing the bighorn population to meet its nutritional needs during this time of year, and prepare for more challenging seasons.

The majority of forbs reached senescence by winter, and were easily covered by snow. Therefore, the general decrease in their diet frequency was expected. Forbs that persisted in the diet were either obtained by pawing through snow or gravel (arrow-leaf balsamroot leaves and tubers and biscuitroot tubers), persisted with a woody base (Eriogonum sp.), or grew along talus slope margins (Phacelia sp.). These forbs maintained crude protein and IVDDM values above grasses, as well as a relatively high Ca content.

Shrubs also reached their highest levels of consumption during summer and late summer-fall, with summer ranking highest. Smith (1954) reported summer as the period of lowest shrub consumption, however, he primarily studied bighorn herds at high elevations during this season. Once again at lower elevations, crude protein content of grasses was declining during this time, while the average crude protein content of shrubs remained constant. The most consistent shrub in the diet was curl-leaf mountain mahogany, which grows primarily on steep rock outcrops and cliffs. Bighorn ewes select such sites during lambing, and the early months of lactation. This habitat selection places ewes in close proximity to this shrub species when new growth is available. Crude protein content of curl-leaf mountain mahogany parts consumed by bighorn ewes averaged approximately 12% during summer and late summer-fall, while crude protein content of grasses had declined to approximately 5% by the end of late summer-fall (Figures 2.2 and 2.4). Tannins have been shown to reduce the availability of protein in some shrub species (Robbins et al. 1987). However, Cook (1990) reported only trace amounts of tannins in true mountain mahogany in Wyoming.

Shrubs contributed the greatest proportion to the diet during winter (52%) along the Clark's Fork River in Montana (Tilton and Willard 1981), and Wikeem and Pitt (1992) reported that bighorns in British Columbia browsed most during winter (18.6%). In central Idaho, Smith (1954) observed bighorns consuming greater amounts of browse during winter months. Hobbs et al. (1981) hypothesized that grasses and shrubs were complimentary components of elk diet during winter. Shrub stems and fallen leaves contained greater levels of crude protein. Yet, grasses provided a more digestible substrate for rumen microbes, because grasses contained less lignin and greater percentages of cellulose and hemicellulose. As a result, grasses contained greater IVDDM, and consequently higher levels of digestible energy (Rittenhouse et al. 1971, Robbins 1993). Protein obtained from shrubs may have maintained a healthy rumen environment for microbes when grasses were low in crude protein. Upon entering winter, ungulates had stored energy reserves in the form of fat. However, Hobbs felt no comparable reserves of amino acids existed. Catabolism of fat reserves resulted in simply weight loss, but negative protein balances resulted in much more serious physiological consequences, such as loss of muscle mass, reduced fetal viability, and decreased disease resistance (Hobbs et al. 1981). The above arguments may apply to bighorn sheep and explain the continued shrub consumption during winter. Perennial bunch grasses were lowest in crude protein and IVDDM during winter and late winter. Bighorns may have entered a negative protein and energy balance without the nutrients supplied by shrubs.

Thaws (and/or rain upon snow) followed by hard freezes periodically left large areas of the winter range covered by sheet ice that prevented bighorns from grazing. Smith (1954) also described this phenomenon. During such occurrences bighorns may retreat to cliffs to browse on shrubs, and take advantage of grasses growing next to large heat absorbing rock outcrops. Such behavior may explain the significantly higher shrub consumption during winter 1995-96, when snow levels were greater than other winters.

Grasses increased to high levels in the diet (73.8%) during winter, and they also were reported to be the major winter forage category by Smith (1954), Blood (1967), Oldemeyer et al. (1971), Dailey et al. (1984), Kasworm et al. (1984), Keating et al. (1985), and Wikeem and Pitt (1992). Bluebunch wheatgrass made up approximately 33% of the diet during this period, the highest percentage for any species at any time of year. Bluebunch wheatgrass peaked in diet frequency during January and February in bighorn diet in British Columbia, where bluebunch wheatgrass culms protruded above the snow, remaining more visible and available than other grasses (Wikeem and Pitt 1992). We also observed increased feeding upon bluebunch wheatgrass during and immediately following snowfall events. Snowfall events were heavier and more frequent during winter and may account for the high diet frequency of bluebunch wheatgrass. Idaho fescue often occurred underneath Douglas-fir canopies. Bighorns frequently would forage in those areas, possibly because snow levels were reduced. Furthermore, average Idaho fescue crude protein content and IVDDM were higher than bluebunch wheatgrass during winter (5.6% versus 4.1%; and 56.6% versus 51.1%, respectively). Bluegrasses and needle-and-thread grass were among the first plants to begin green-up. On southern exposures and/or near sources of heat, such as rock outcrops, bluegrasses began showing signs of green growth during the latter weeks of winter. Crude protein content averaged 16.3% for new growth compared to 3.6% for senescent bluegrass material, and bighorns quickly utilized these species.

By spring green-up shrub diet frequency dropped to its lowest levels (3.9%) and grass diet frequency peaked (79.9%). Smith (1954) reported a similar increase in grasses and a decrease in shrub consumption during spring. During this period, crude protein and IVDDM levels of grasses were at all time highs, averaging 21.7% and 79.1%, respectively. Bighorn sheep when presented with high quality grass forage concentrated on this category. During other periods, bighorn may have utilized shrubs to obtain protein in spite of potentially higher lignin levels. Increased shrub consumption resulted in increased mean retention times in the rumen for both grasses and browse (Baker and Hobbs 1987). Once lignin-free protein sources, i. e. grasses, were abundant bighorn switched to sources better suited to their evolved digestive physiology. Such abundant nutrients appear at a critical time for adult ewes. Fetal growth follows a non-linear exponential trajectory with the greatest growth occurring during the third trimester. Parturition is soon followed by the even more demanding nutrient requirements of lactation (Robbins 1993).

Several elements, such as phosphorous, potassium, sulfur, magnesium, copper, and zinc, generally followed an annual cycle of abundance similar to crude protein levels in grasses. Certain of these elements, such as sulfur, are chemical constituents of amino acids. For proper absorption and metabolism calcium to phosphorous ratios should range from 1:1

to 2:1 (Robbins 1993). Phosphorous levels may decrease to low levels over winter while calcium levels remain relatively stable, thus producing a high ratio (Demarchi 1968). Excesses of calcium do not affect phosphorous absorption as much as phosphorous excesses affect calcium absorption (Robbins 1993).

Nutrient requirements for macro and micro minerals, have not been experimentally determined for bighorn sheep, and authors have used values established for domestic sheep. However, Robbins (1993) argued that wild animals have faced entirely different selection pressures from those of domestic animals, and consequently would not be expected to have similar nutrient requirements. The data presented here may be helpful in determining the season(s) when bighorn sheep are most likely to experience a deficiency in these nutrients; specifically mid- to late-winter and early spring. However, when certain trace elements, such as selenium, chromium, and cobalt, are almost entirely absent from forage samples collected from grasses, forbs, and shrubs one may be justified in concluding that these important trace minerals are deficient in the diet of bighorn sheep in Big Creek.

MANAGEMENT IMPLICATIONS

Temporal changes in bighorn diet at lower elevations in Big Creek strengthen the premise that bighorn sheep are able to adapt diet selection patterns to meet nutritional needs. Although grasses make up the majority of plants consumed, forbs and shrubs may furnish high quality nutrients at key times during the year. Managers should focus on providing a diversity of plant species in all forage categories.

Nonexistent to very low levels of certain essential trace elements in most all forage species raises additional questions. For example, do bighorn sheep obtain these nutrients from mineral licks? If not, perhaps managers may enhance the nutritional status of bighorn sheep in the area by providing mineral supplements at key locations.

Exotic weeds such as spotted knapweed (Centaurea maculosa) are beginning to invade the Big Creek winter range. Such exotic invasions may result in a decrease in plant species diversity (Whitson et al. 1996). If low-elevation bighorn herds rely on a diverse plant community to meet their nutritional needs, then these exotic invaders may be a serious threat to future generations of bighorn sheep.

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Table 2.1 Average period[a] composition of plant species (≥ 1%) in bighorn sheep diet and standard error (SE) as determined by microhistological fecal analysis from Big Creek, Idaho 1994-1997.

	Period									
Plant	Summer		Late Summer-Fall		Winter		Late Winter		Spring Green-up	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
Graminoids	48.4	5.2	48.0	9.2	73.8	4.4	66.0	6.4	79.9	3.9
Pseudoroegnenia spicata	14.9	2.4	23.3	5.4	33.0	3.5	23.6	4.0	22.2	4.1
Bromus tectorum	5.5	1.4	2.2	0.8	3.4	0.6	1.8	0.5	2.4	1.1
Bromus sp.	1.2	0.4	0.0		1.1	0.3	4.4	0.7	4.1	1.2
Festuca idahoensis	6.6	1.6	3.0	0.9	6.2	0.6	7.0	1.3	12.4	1.5
Koleria cristata	1.1	0.5	2.3	0.7	2.5	0.9	0.8	0.3	1.6	0.6
Poa sp.	8.8	1.4	7.4	1.5	10.5	1.1	9.8	0.8	14.4	1.2
Sitanion hystrix	0.0		0.0		0.7	0.3	1.1	0.3	0.7	0.3
Hesperochloa comata	7.3	1.0	8.2	1.5	14.8	1.2	14.5	2.8	16.9	2.5
Other grasses	2.5	0.4	1.3	0.5	1.4	0.4	2.4	0.8	3.3	0.8
Forbs	28.7	4.7	33.5	6.7	11.3	2.5	13.0	2.0	11.6	2.4
Achillea millefolium	3.1	1.4	2.4	0.5	0.4	0.2	0.3	0.2	0.5	0.2
Arabis/Thelypodium	1.7	0.6	8.1	2.5	0.6	0.3	0.6	0.3	0.5	0.3
Astragalus sp.	1.9	0.3	1.8	0.6	0.2	0.1	0.3	0.2	0.3	0.1
Balsamorhiza sagitata	0.5	0.3	0.2	0.1	3.4	1.3	6.6	1.3	4.7	2.2
Cirisium sp.	2.3	0.6	0.5	0.3	0.4	0.4	0.2	0.2	0.2	0.2
Descurainia pinnata	0.1	0.1	1.0	0.4	0.0		0.0		0.2	0.1
Epilobium sp.	0.8	0.6	1.1	0.5	0.0		0.0		0.0	
Equisetum sp.	1.2	1.0	0.1	0.1	0.0		0.0		0.0	

Table 2.1 Continued.

	Period									
Plant	Summer		Late Summer-Fall		Winter		Late Winter		Spring Green-up	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
Erigeron sp.	0.4	0.2	2.4	0.7	0.0		0.1	0.1	0.2	0.2
Eriogonum sp.	0.7	0.3	1.8	0.5	0.3	0.2	1.3	0.8	0.7	0.4
Lesquerella sp.	0.4	0.3	6.4	2.4	0.3	0.1	0.0		0.1	0.1
Lupinus sp.	0.7	0.4	2.1	0.8	0.6	0.2	0.7	0.3	0.9	0.3
Penstemon sp.	1.3	0.6	0.9	0.5	0.2	0.1	0.1	0.1	0.0	
Phacelia sp.	2.7	0.8	0.1	0.1	1.0	0.4	0.3	0.1	0.3	0.1
Other forb	3.3	0.6	3.1	0.6	1.0	0.2	1.5	0.5	1.4	0.4
Browse	21.9	2.0	18.4	3.5	14.9	2.6	12.3	4.3	3.9	1.4
Amalanchier alnifolia	0.0		1.1	0.8	0.3	0.2	0.4	0.2	0.2	0.2
Berberis repens	0.4	0.3	2.1	1.0	0.9	0.3	1.6	0.6	0.5	0.4
Cercocarpus ledifolius	6.1	1.5	0.2	0.1	6.1	2.1	6.1	2.5	1.1	0.5
Physocarpus malvaceus	2.8	1.5	1.2	0.6	0.1	0.1	0.2	0.1	0.5	0.3
Purshia tridentata	6.8	1.5	9.1	2.3	4.3	1.3	1.4	0.5	0.7	0.4
Ribes sp.	1.9	0.7	0.0		0.1	0.1	0.0		0.1	0.1
Salix sp.	0.6	0.4	0.8	0.2	0.7	0.3	1.8	1.4	0.1	0.1
Conifer	0.34	0.3	0.0		1.4	0.7	8.1	2.9	3.4	1.1
Pseudotsuga menziesii	0.0		0.0		1.0	0.4	7.3	3.0	3.2	1.0
Other										
Moss	0.0		0.0		0.1	0.1	1.1	0.5	0.9	0.3

[a] Summer = 1 June to 15 Aug., Late Summer-Fall = 16 Aug. to 15 Nov., Winter = 16 Nov. to 15 Feb., Late Winter = 16 Feb. to 31 March, Spring Green-up = 1 April to 31 May.

Table 2.2 Spearman's rank correlation coefficients (ρ) and Renkonen percentage similarity indexes comparing period diets[a].

Periods[b]	Spearman's		Percent similarity
	ρ	*P*	
1 vs. 2	0.477	0.003	67.04
1 vs. 3	0.532	0.001	67.15
1 vs. 4	0.318	0.063	62.71
1 vs. 5	0.385	0.022	59.56
2 vs. 3	0.325	0.057	61.84
2 vs. 4	0.209	0.228	58.27
2 vs. 5	0.300	0.081	57.41
3 vs. 4	0.877	0.001	79.79
3 vs. 5	0.815	0.001	75.15
4 vs. 5	0.887	0.001	82.15

[a] *n* = 34 for all tests.

[b] Period 1 = summer (1 June to 15 Aug.), Period 2 = late summer-fall (16 Aug. to 15 Nov.), Period 3 = winter (16 Nov. to 15 Feb.), Period 4 = late winter (16 Feb. to 31 March), Period 5 = spring green-up (1 April to 31 May).

Figure 2.1 Percent diet composition of grasses, forbs, and browse in the diet of bighorn sheep from Big Creek, Idaho 1994-97

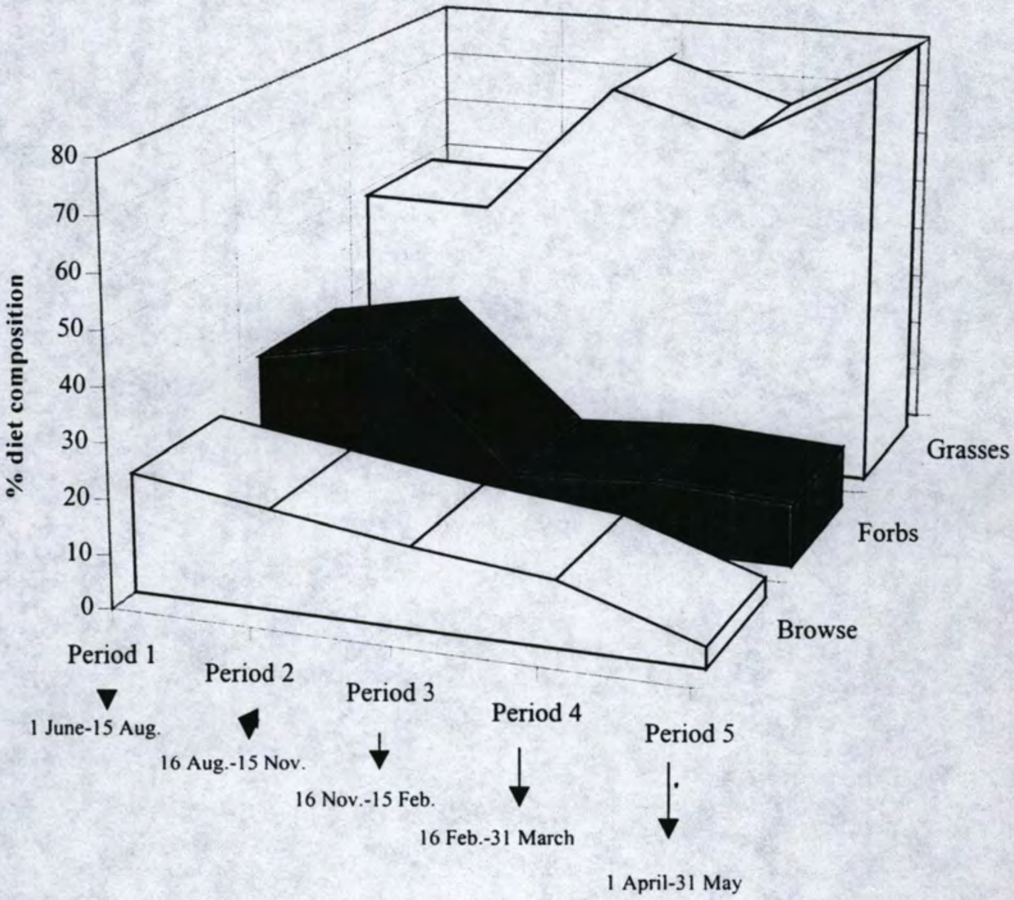


Figure 2.2 Polynomial regression of % crude protein on period for grasses collected from Big Creek, Idaho 1994-97

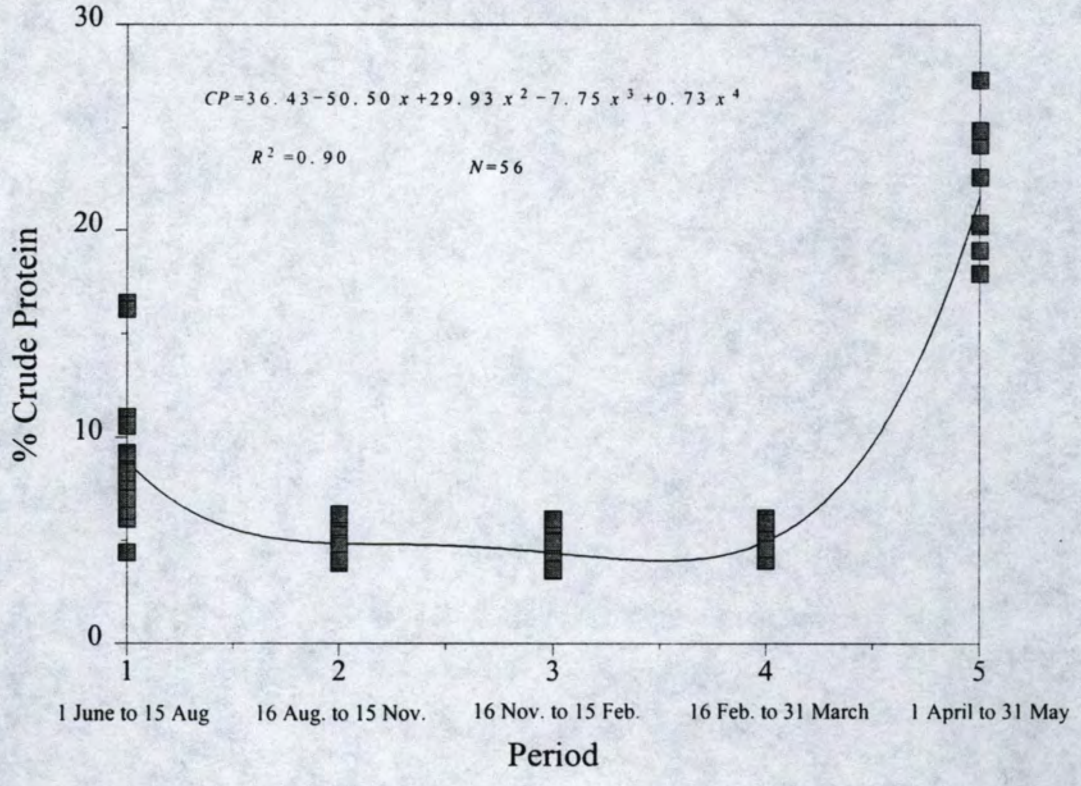


Figure 2.3 Polynomial regression of % crude protein content on period for forbs collected from Big Creek, Idaho 1994-97

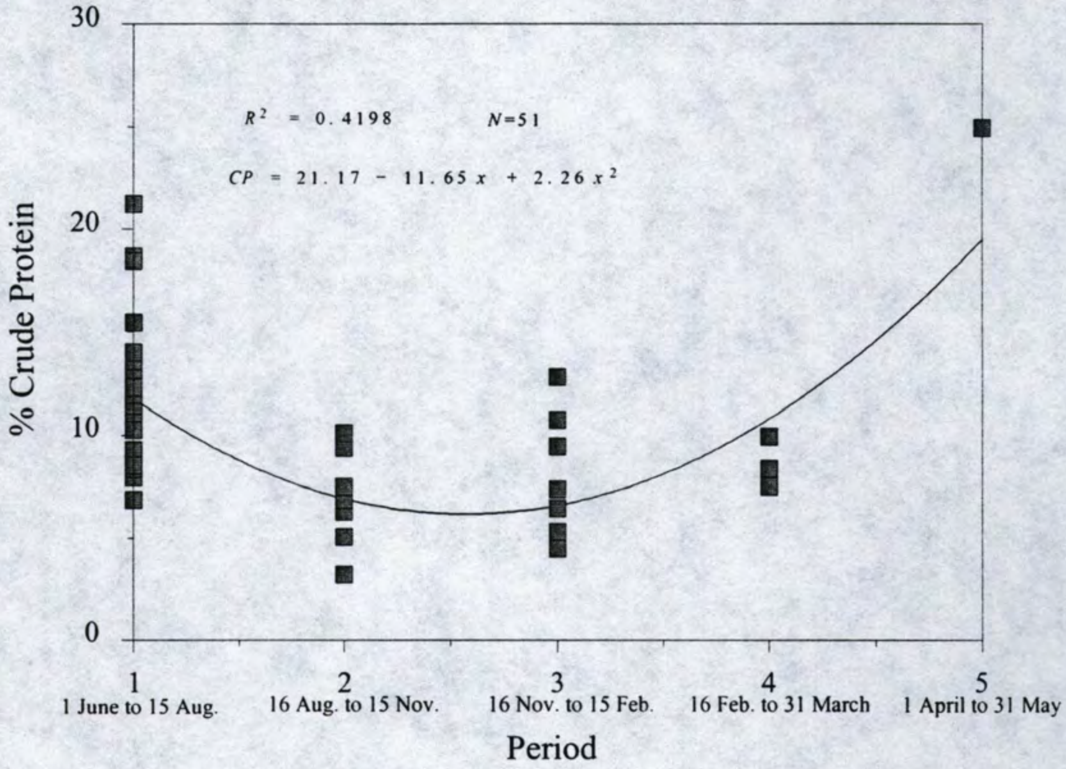


Figure 2.4 Linear regression of % crude protein on period for shrubs collected from Big Creek, Idaho 1994-97

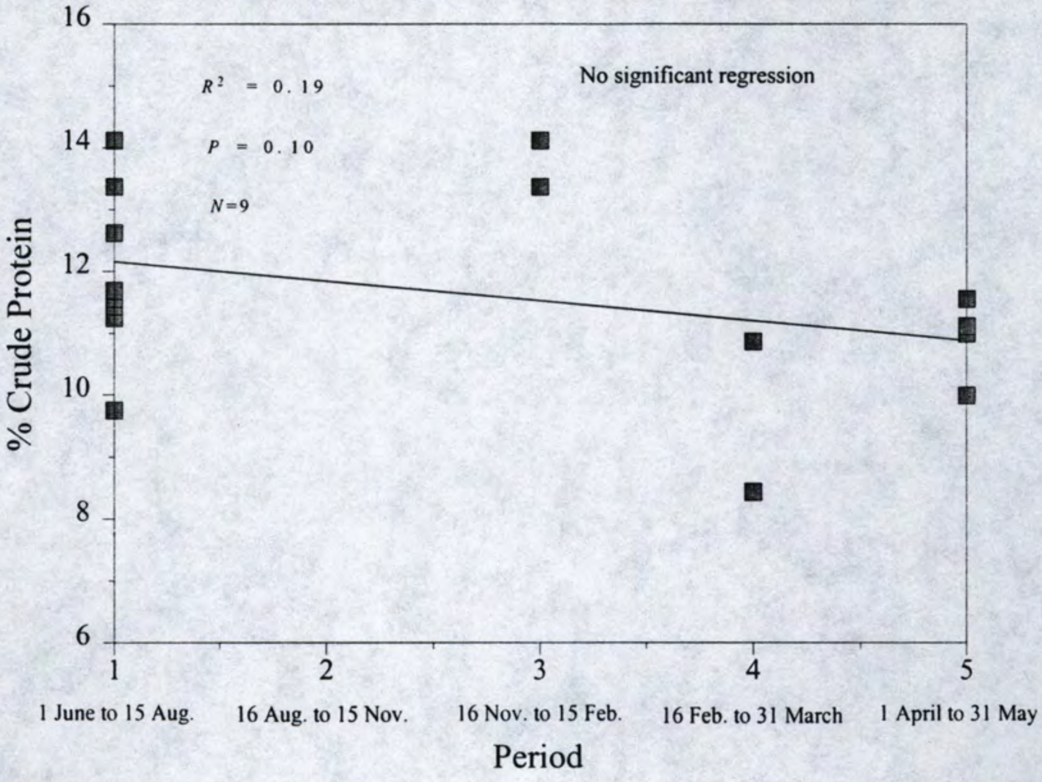


Figure 2.5 Polynomial regression of % in vitro digestible dry matter on period for grasses collected from Big Creek, Idaho 1994-97

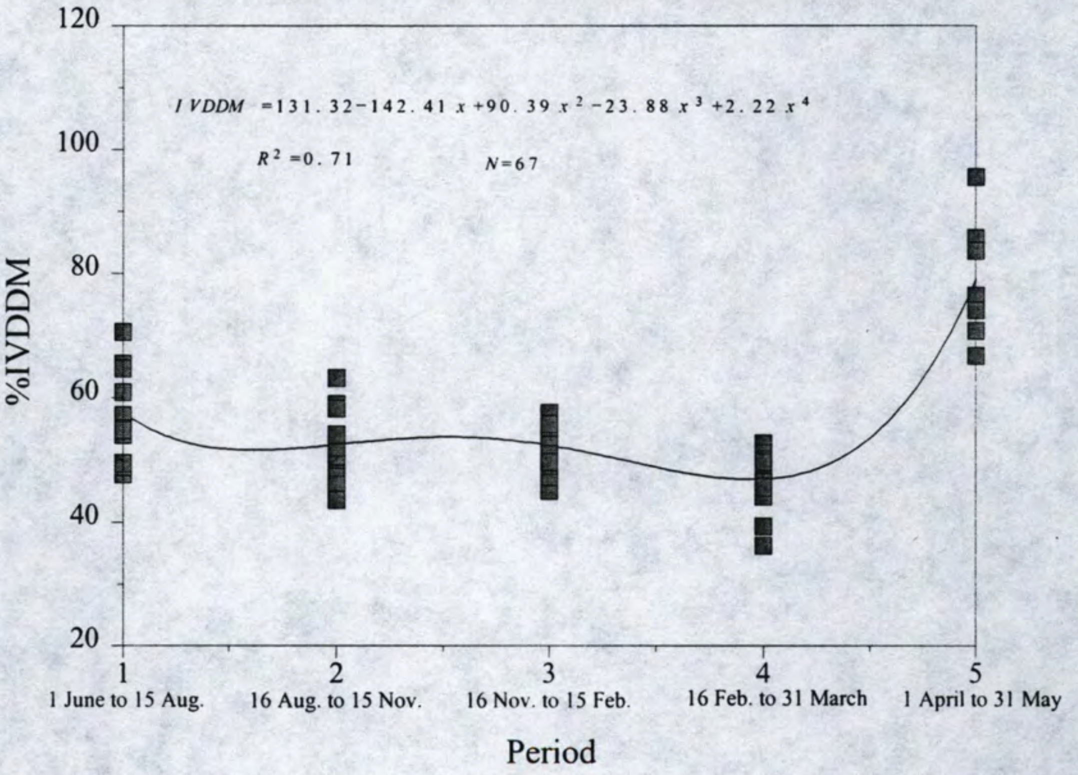


Figure 2.6 Polynomial regression of % in vitro digestible dry matter on period for forbs collected from Big Creek, Idaho 1994-97

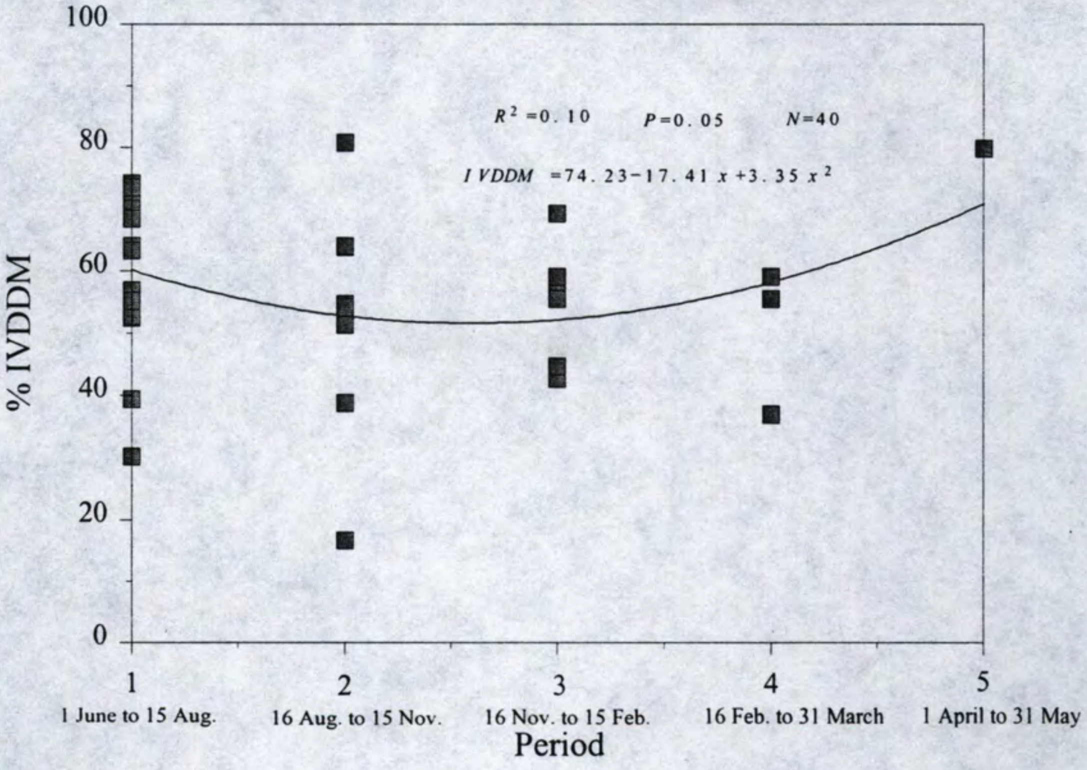


Figure 2.7 Linear regression of % in vitro digestible dry matter on period for shrubs collected from Big Creek, Idaho 1994-97

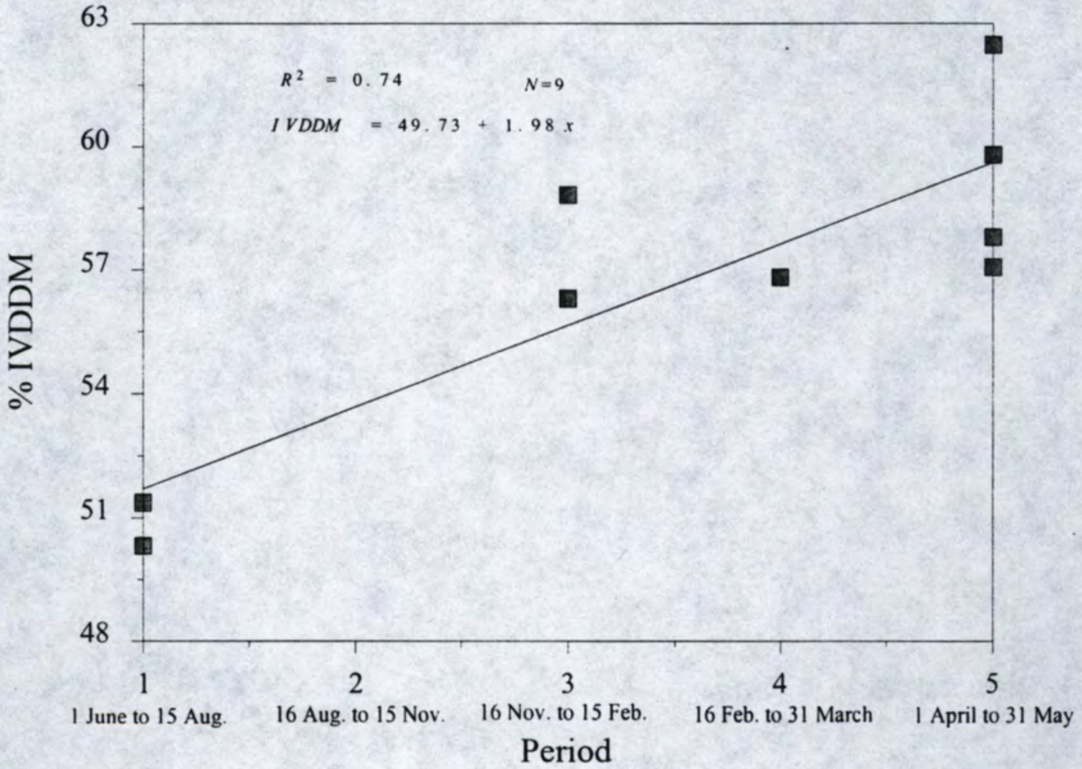


Figure 2.8 Polynomial regression of Phosphorus content on period for grasses collected from Big Creek, Idaho 1994-97

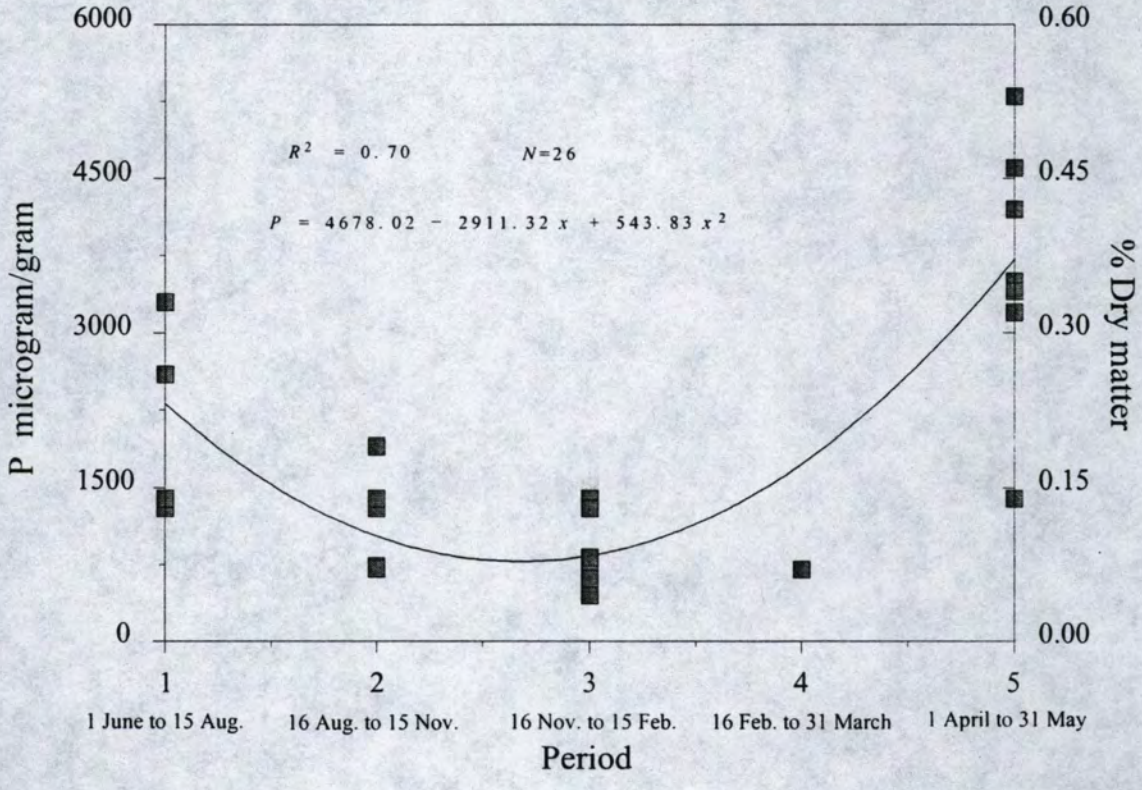


Figure 2.9 Polynomial regression of Phosphorus content on period for forbs collected from Big Creek, Idaho 1994-97

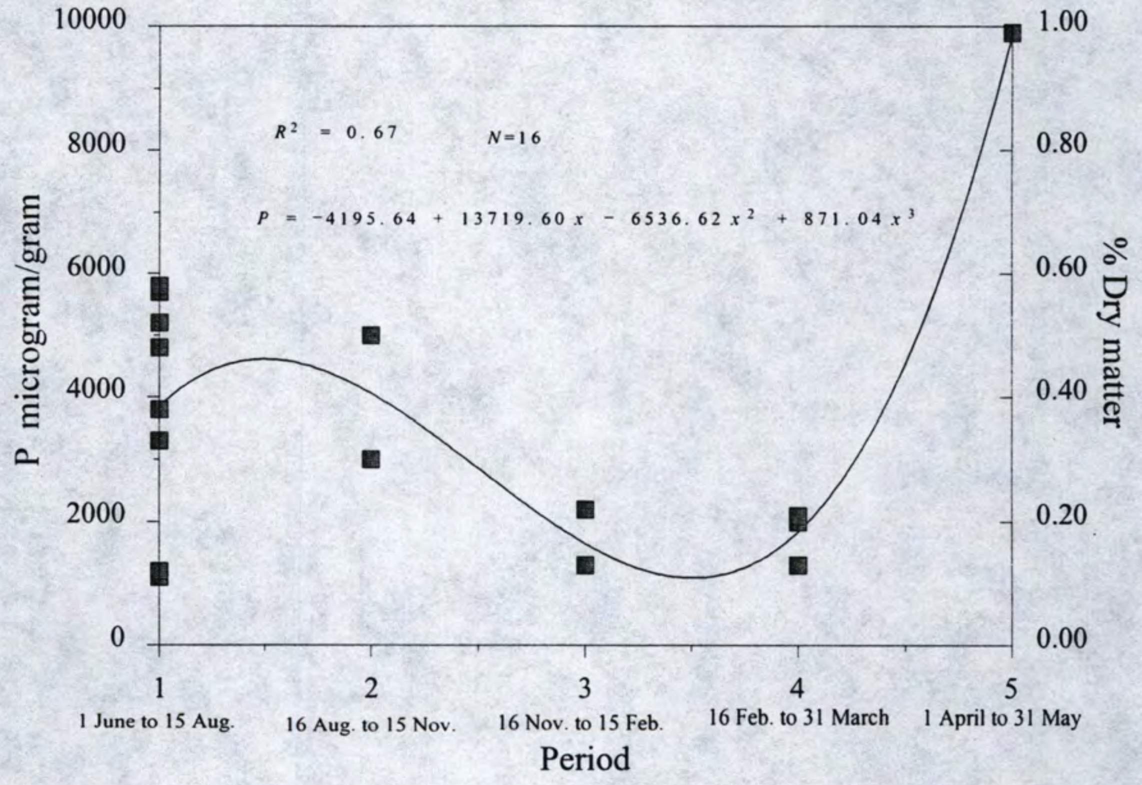


Figure 2.10 Polynomial regression of Phosphorus content on period for shrubs collected from Big Creek, Idaho 1994-97

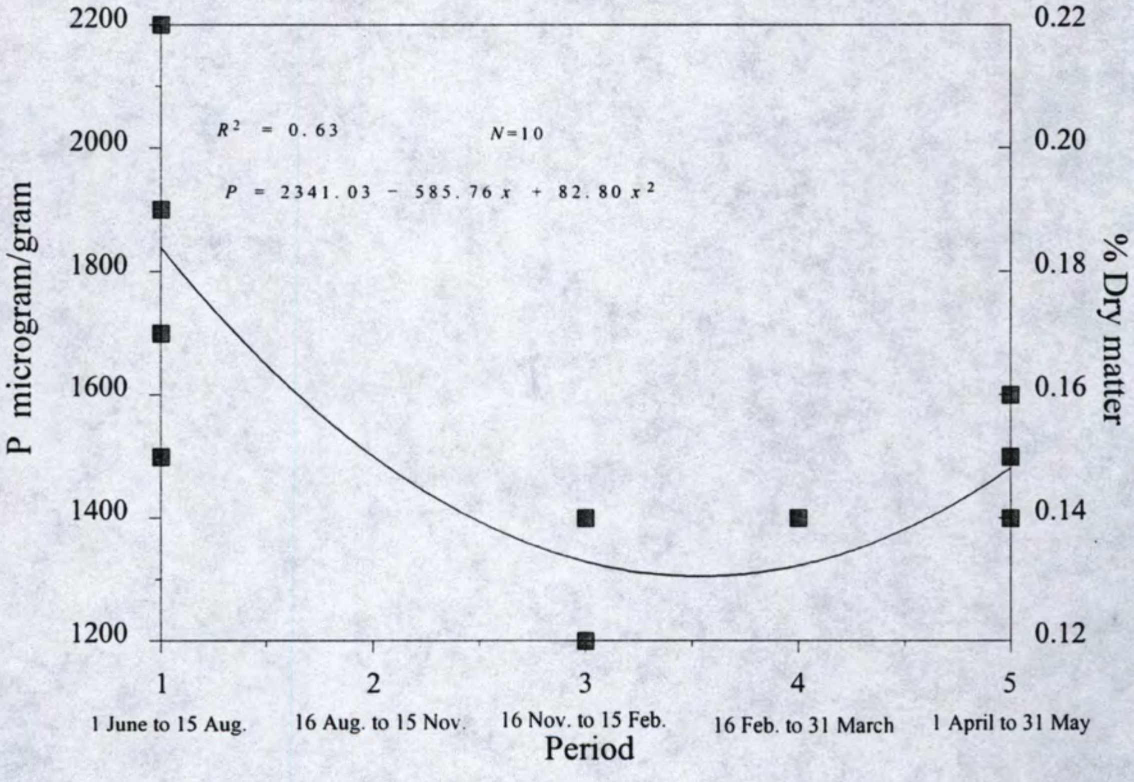


Figure 2.11 Polynomial regression of Potassium content on period for grasses collected from Big Creek, Idaho 1994-97

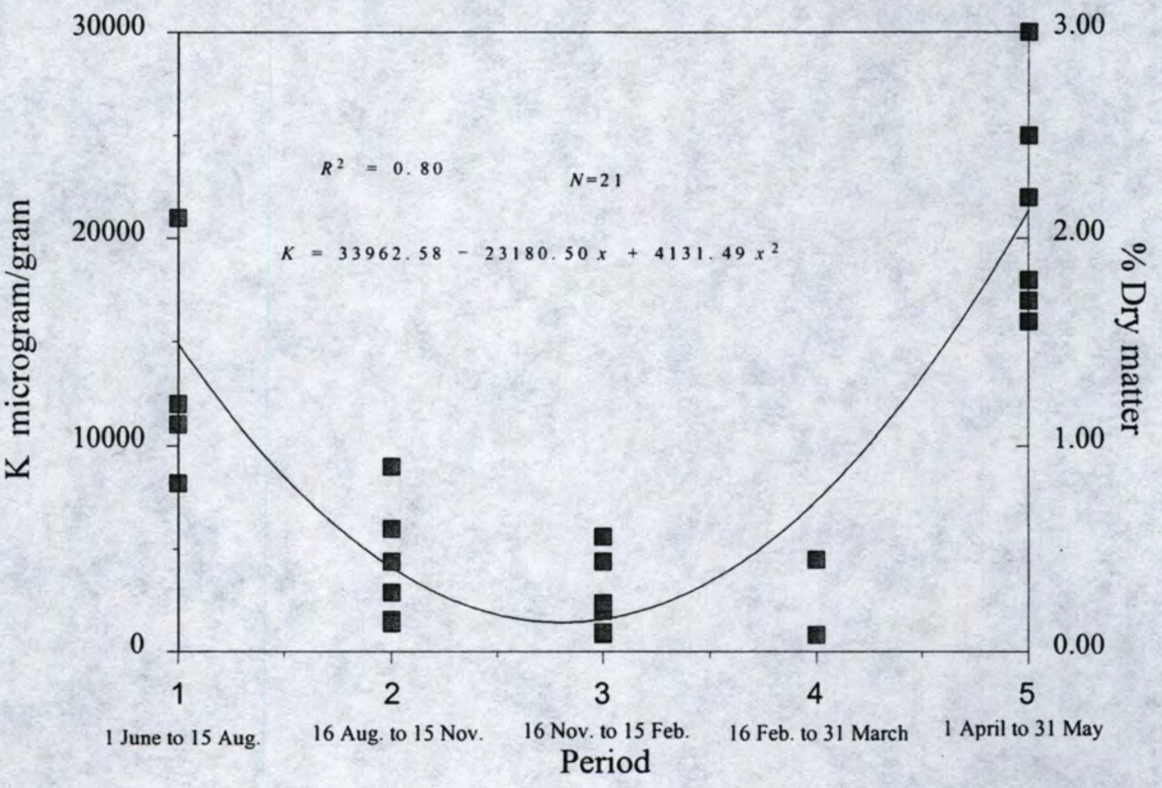


Figure 2.12 Polynomial regression of Potassium content on period for forbs collected from Big Creek, Idaho 1994-97

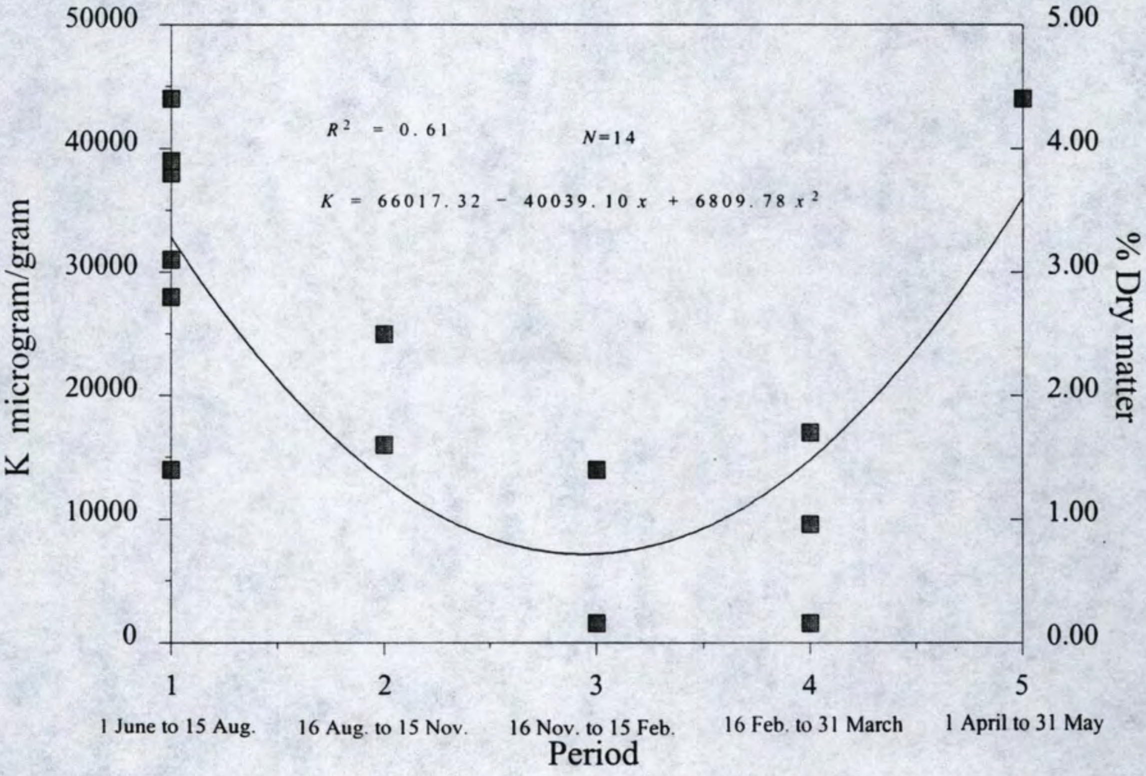


Figure 2.13 Polynomial regression of Potassium content on period for shrubs collected from Big Creek, Idaho 1994-97

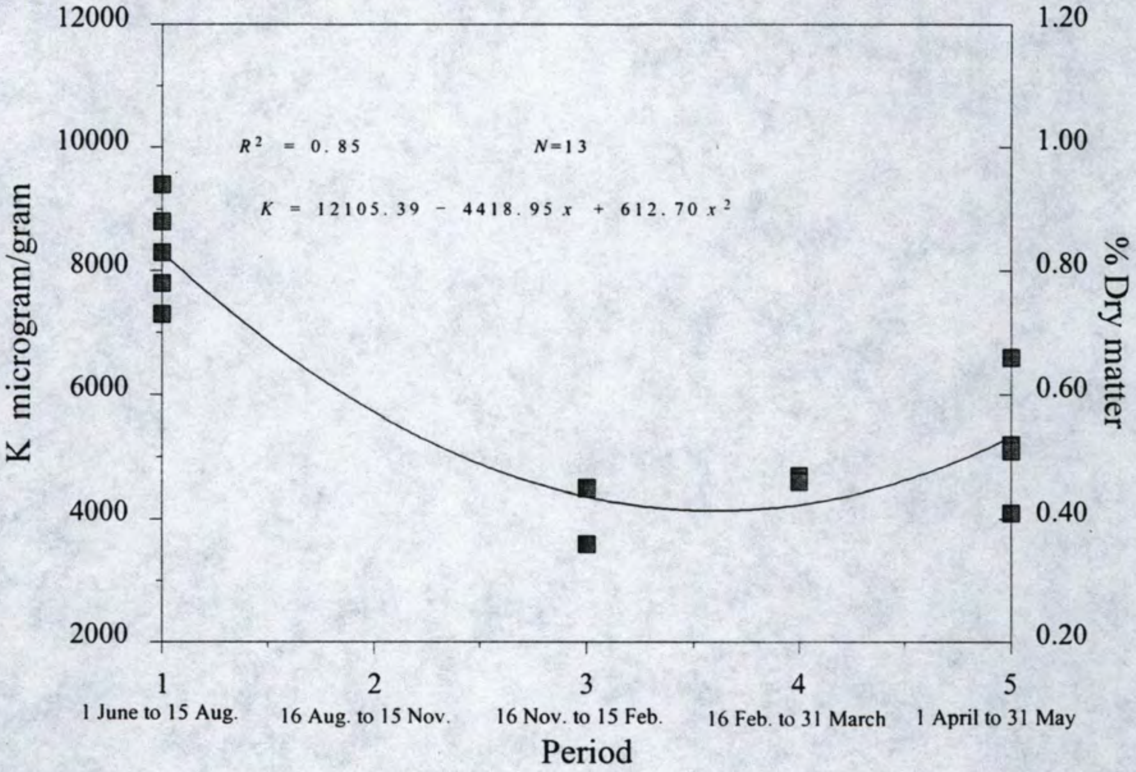


Figure 2.14 Polynomial regression of Sulfur on period for grasses collected from Big Creek, Idaho 1994-97

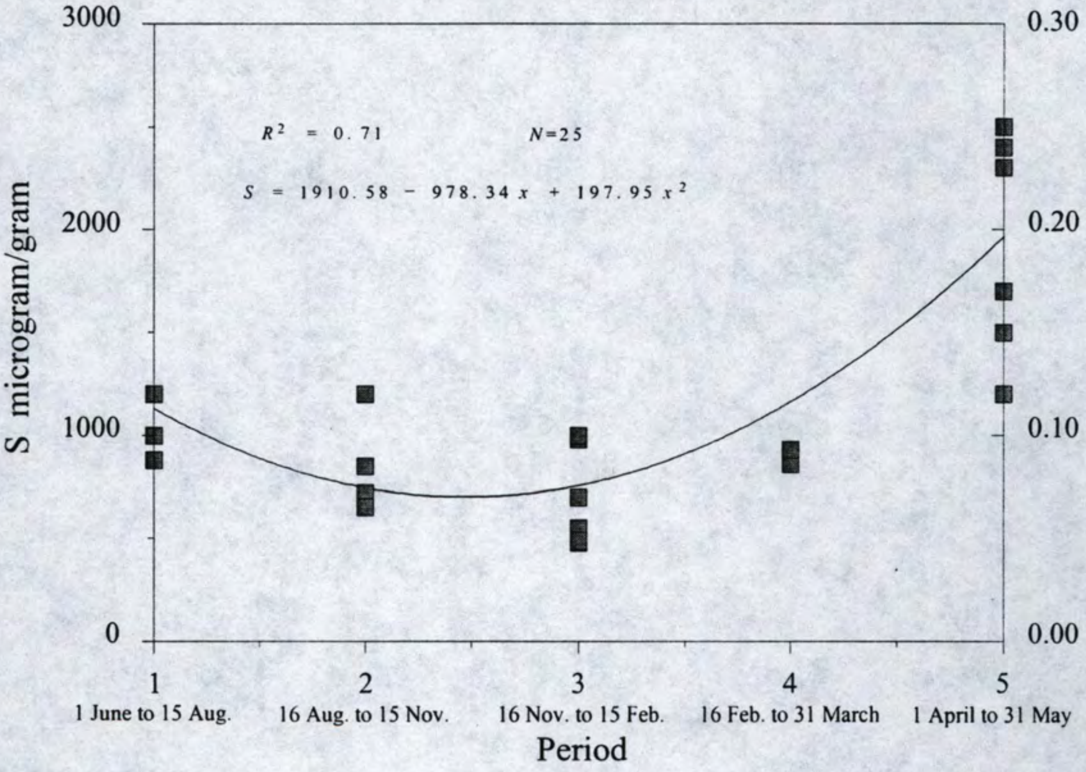


Figure 2.15 Polynomial regression of Sulfur content on period for forbs collected from Big Creek, Idaho 1994-97

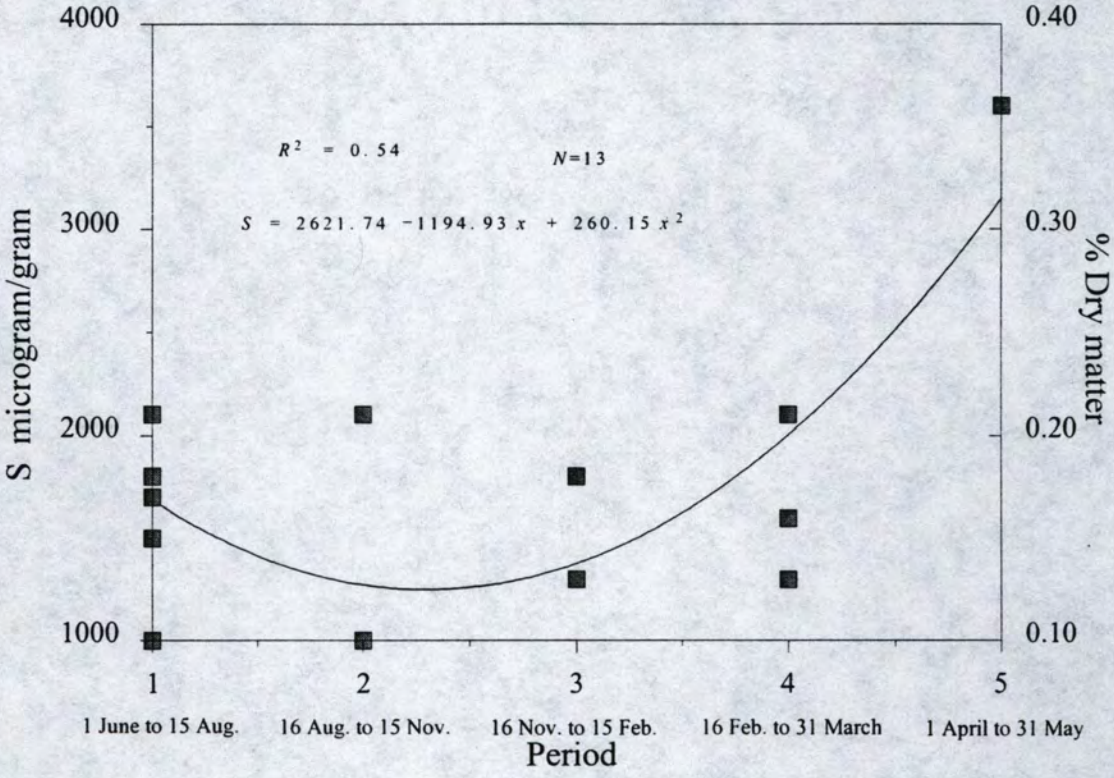


Figure 2.16 Polynomial regression of Sulfur content on period for shrubs collected from Big Creek, Idaho 1994-97

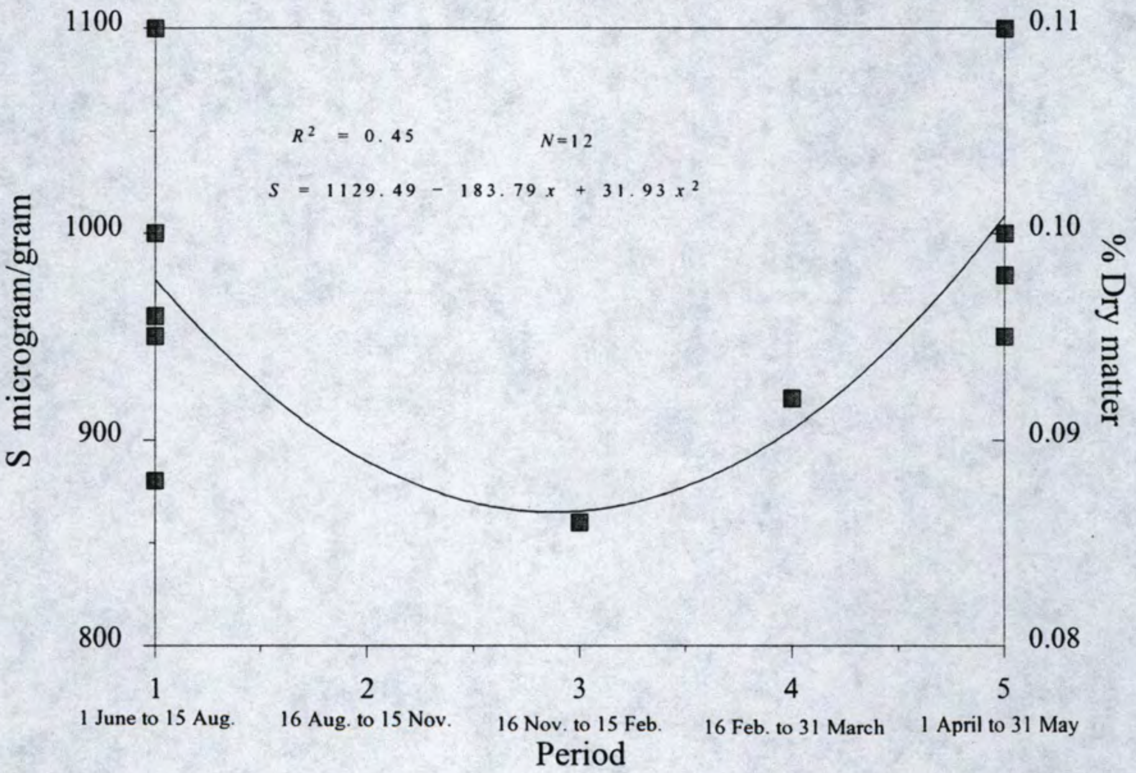


Figure 2.17 Polynomial regression of Magnesium on period for grasses collected from Big Creek, Idaho 1994-97

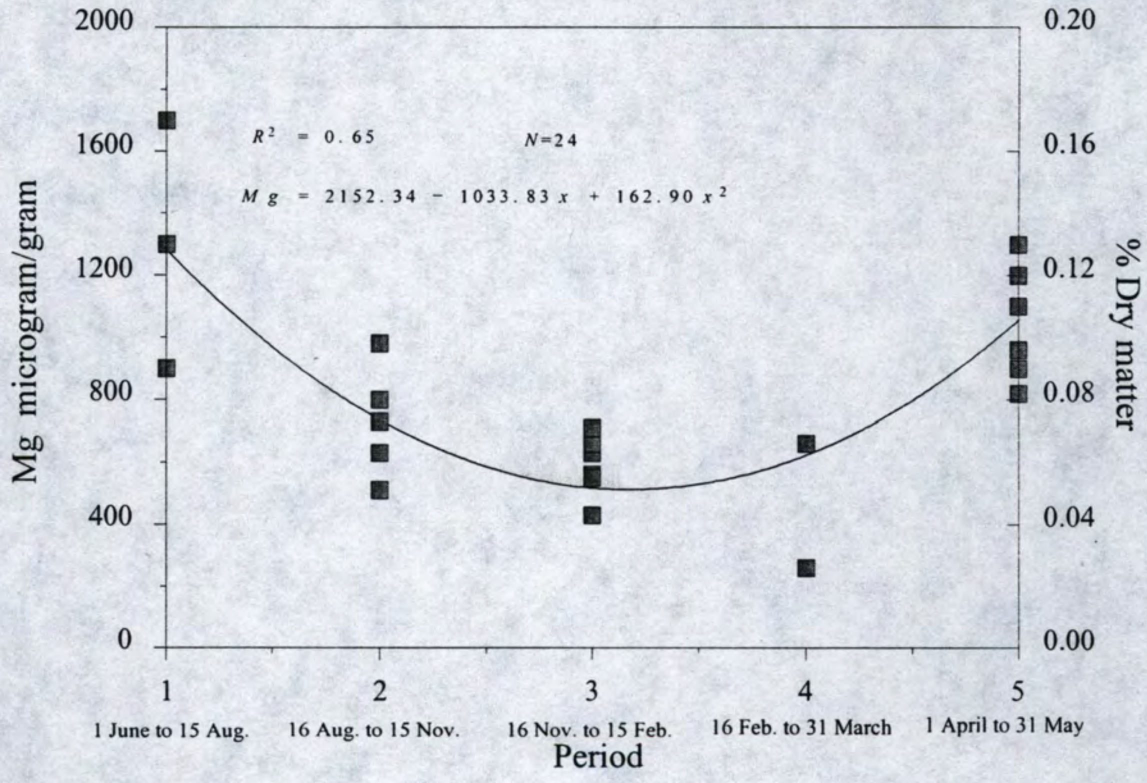


Figure 2.18 Polynomial regression of Magesium content on period for forbs collected from Big Creek, Idaho 1994-97

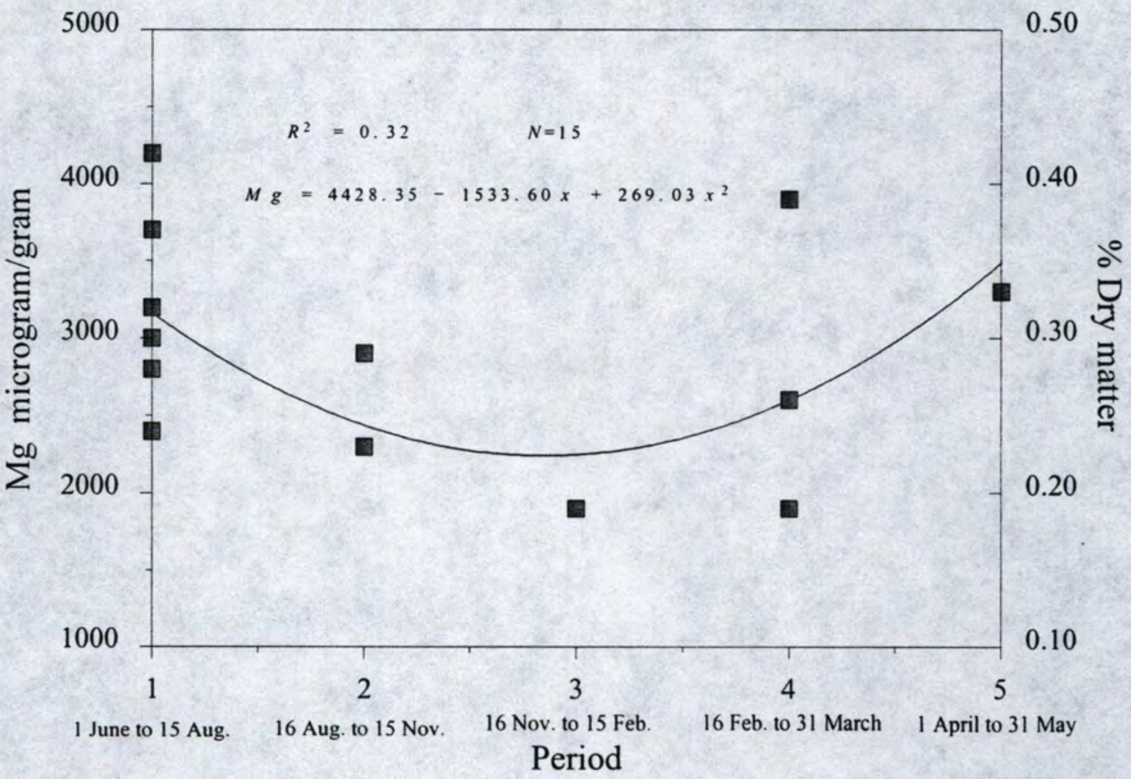


Figure 2.19 Polynomial regression of Copper content on period for grasses collected from Big Creek, Idaho 1994-97

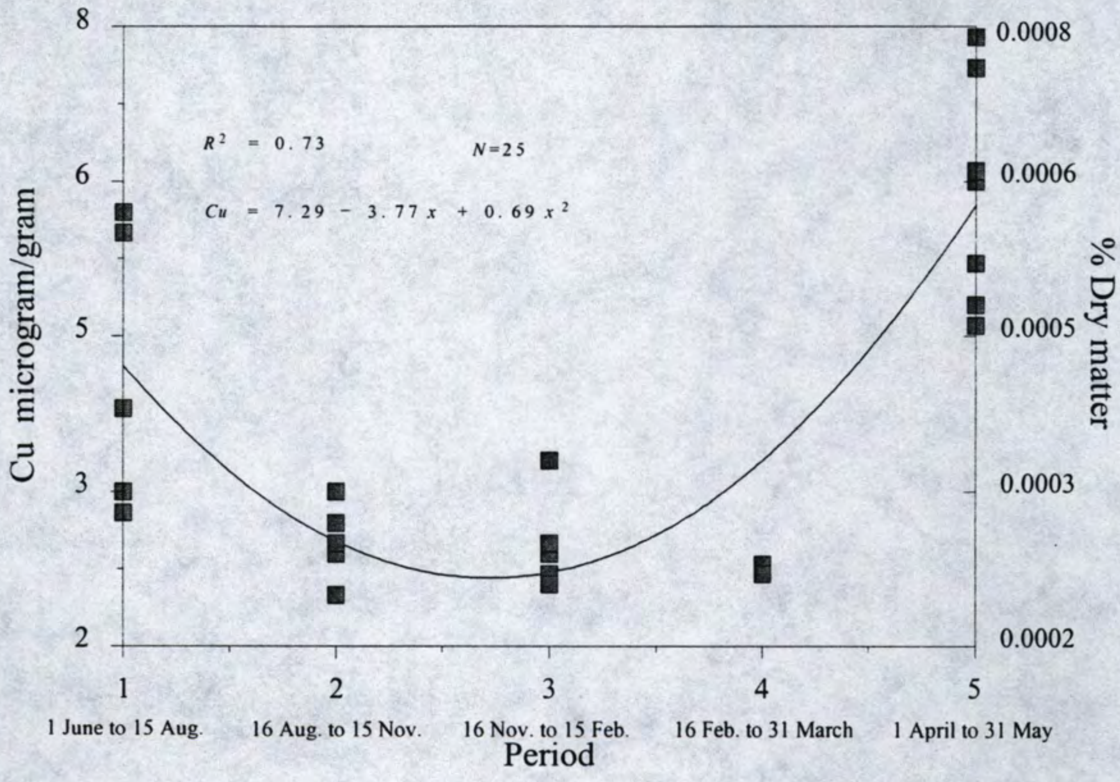


Figure 2.20 Polynomial regression of Copper content on period for shrubs collected from Big Creek, Idaho 1994-97

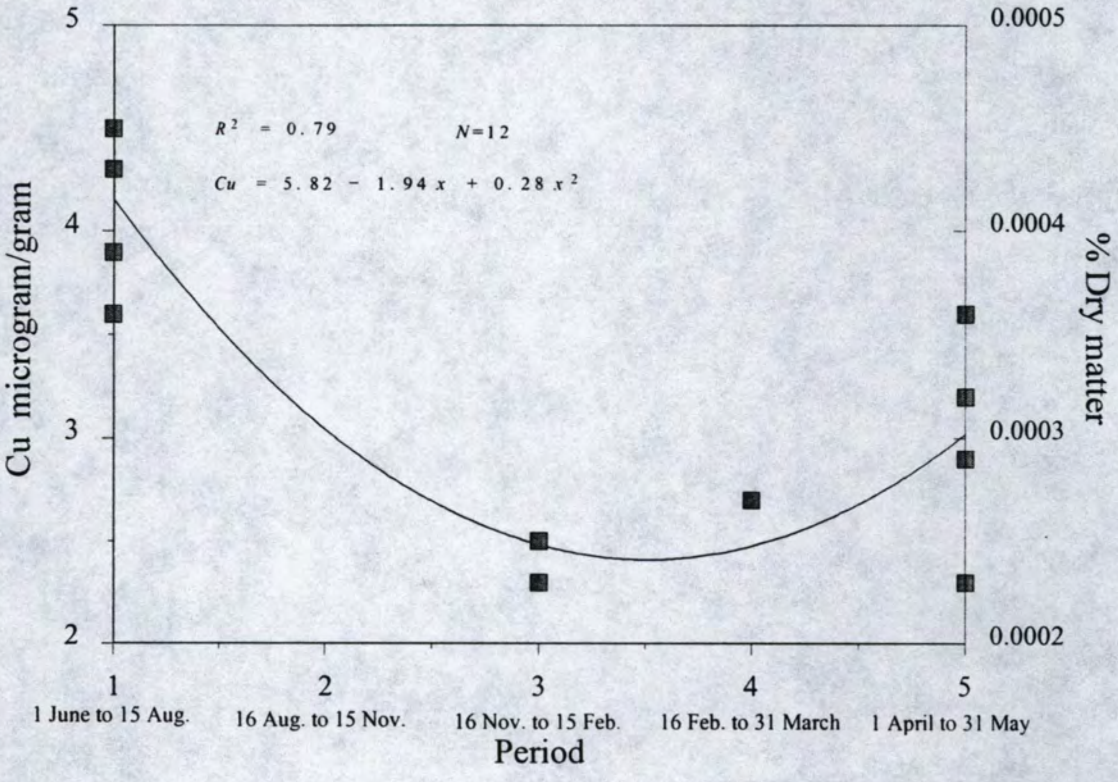


Figure 2.21 Polynomial regression of Zinc content on period for grasses collected from Big Creek, Idaho 1994-97

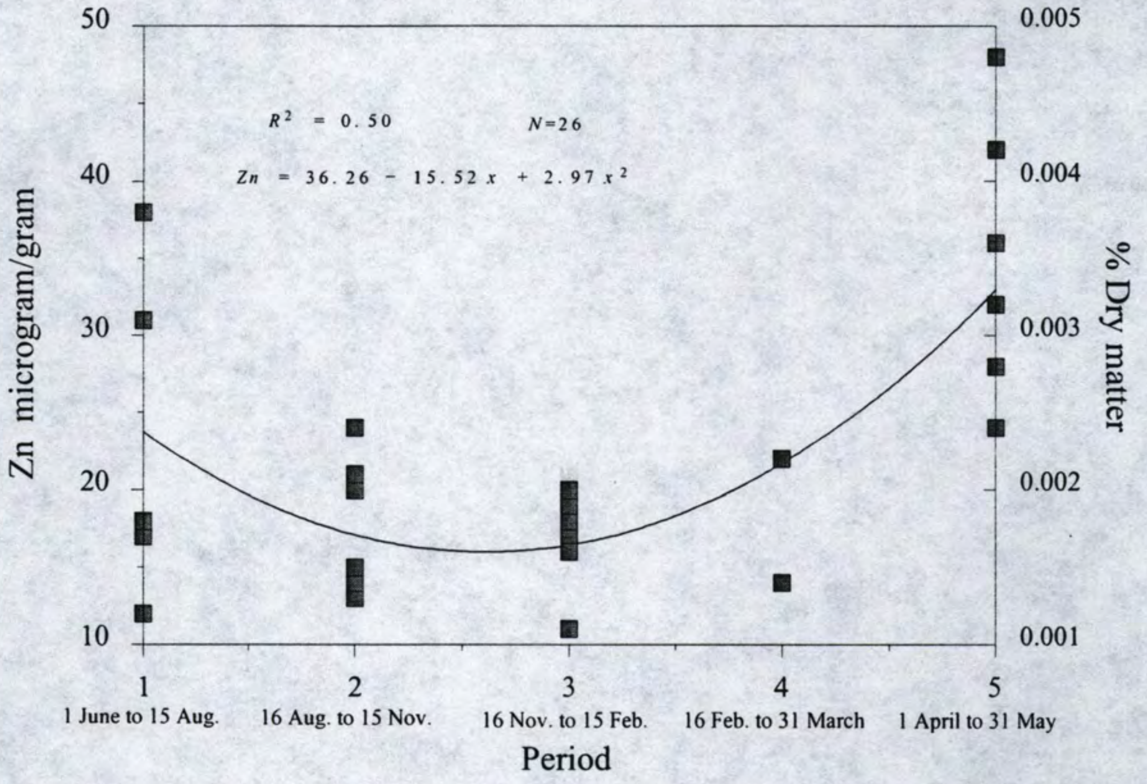


Figure 2.22 Polynomial regression of Calcium content on period for shrubs collected from Big Creek, Idaho 1994-97

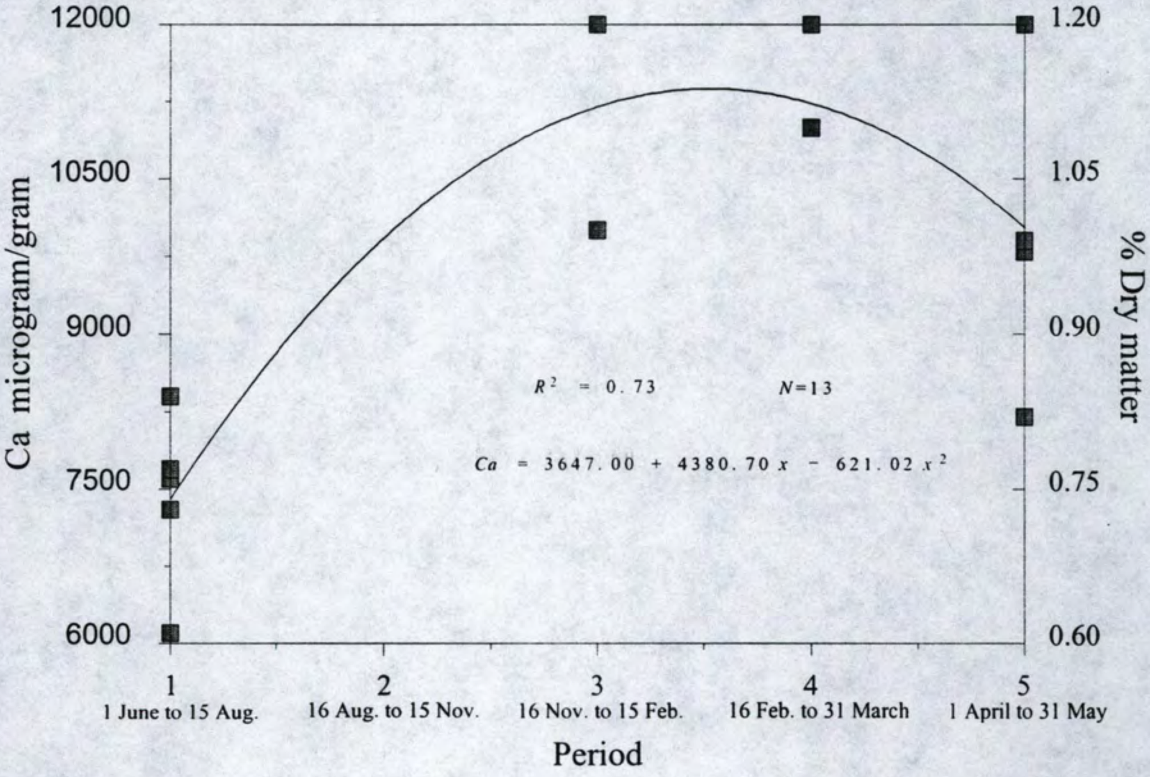


Figure 2.23 Polynomial regression of Calcium:Phosphorus ratio on period for grasses collected from Big Creek, Idaho 1994-97

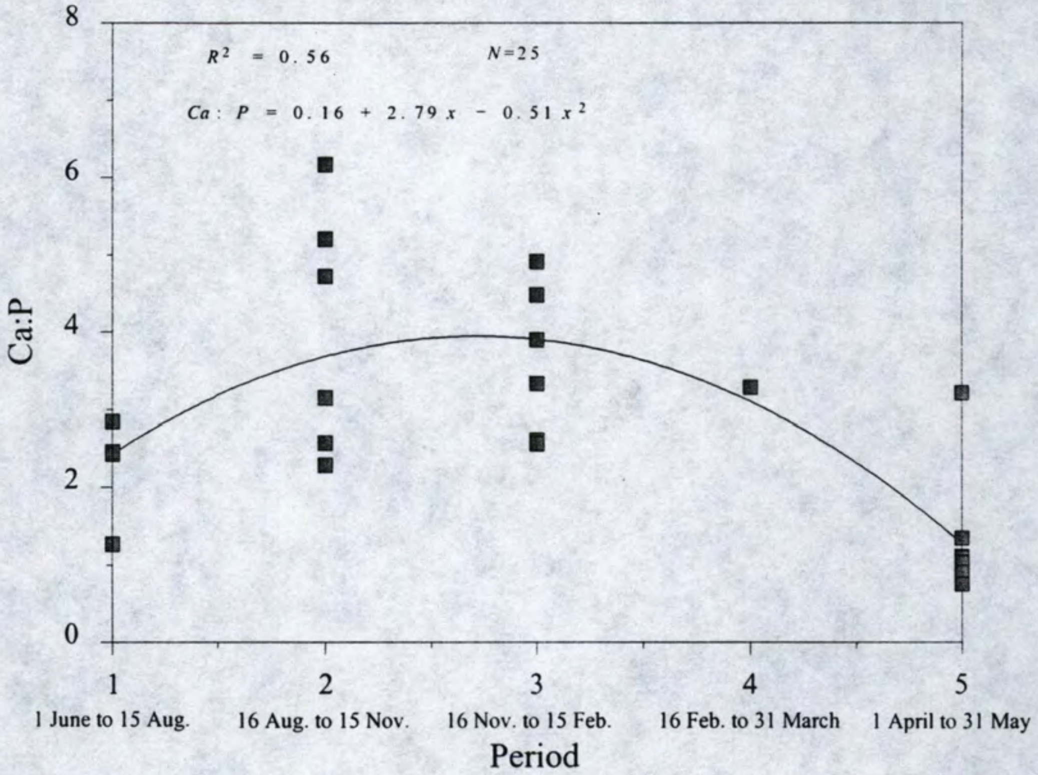
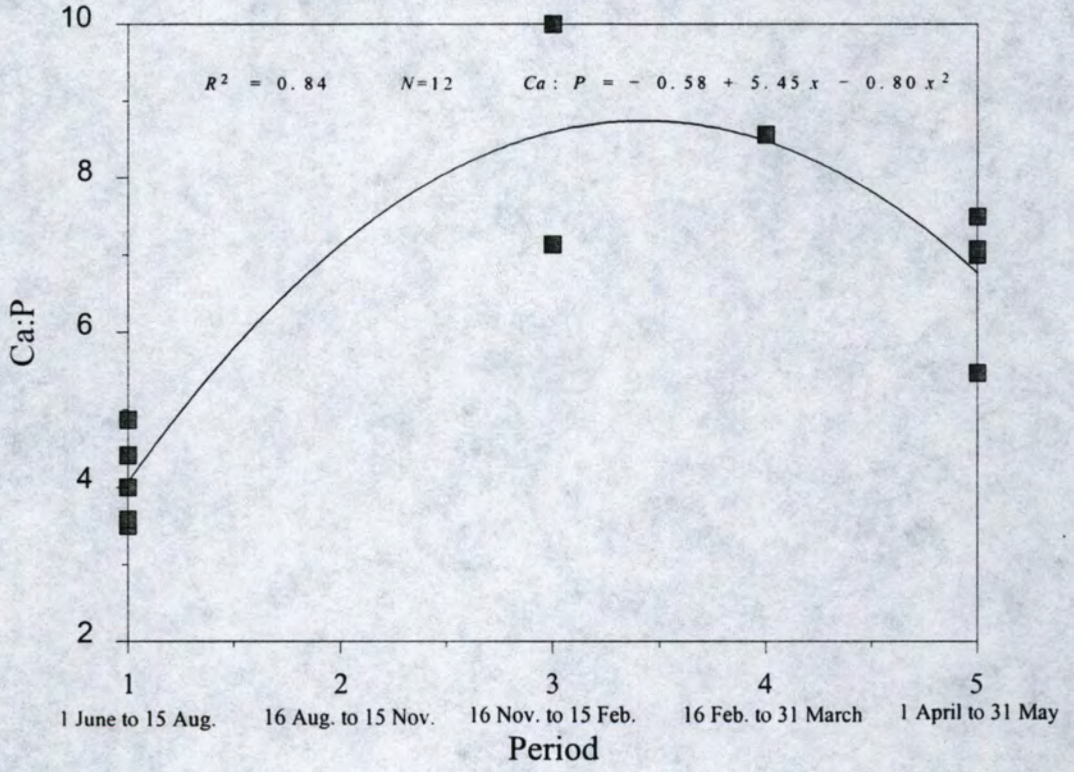


Figure 2.24 Polynomial regression of Calcium:Phosphorus ratio on period for shrubs collected from Big Creek, Idaho 1994-97



Chapter 3

Activity Patterns of Rocky Mountain Bighorn Ewes in Central Idaho

INTRODUCTION

Activity patterns may reveal how animals deal with changing environmental influences and nutrient sources. Furthermore, estimation of energy requirements necessitates a knowledge of activity patterns. Estimates of energy requirements coupled with a knowledge of energy intake allows assessment of a population's nutritional status in terms of energy. Such knowledge may explain foraging strategies and trophic dynamics. Knowledge of activity patterns also may help managers plan aerial surveys to coincide with time periods when animals are most active and visible, and delineate seasons and daily time periods when animals are most vulnerable to human disturbance.

Bighorn sheep (Ovis canadensis) activity patterns have been studied by Mills (1937), Davis (1938), Blood (1963), Woolf et al. (1970), Geist (1971), Van Dyke (1978), Eccles (1978, 1983), Stemp (1983), Belovsky and Slade (1986), Goodson et al. (1991), and Sayre and Seabloom (1994). However, Shakleton et al. (1999 p 108) stated "Available information on activity patterns and the ecological factors influencing them are still very limited for Rocky Mountain and California bighorn".

Most authors reported from 2-4 daily activity peaks. Geist (1971) noted activity peaks were closer to mid-day in winter months compared to summer, presumably, in response to higher temperatures. Smith (1954) observed the daily activities of bighorn sheep in central Idaho. He found bighorns generally lacked a strict routine, but usually bedded following morning and mid-day feeding bouts. He had difficulty determining the effects of environmental variables on bighorn behavior. Neither weather nor season appeared to influence activity patterns, except during periods of deep snow. Bighorns spent more time feeding, because they were forced to paw through snow to obtain adequate forage. Detailed time-budgets that included nocturnal behavior were not developed for bighorn sheep on the study area.

The objectives of the study were to collect activity data on adult non-migratory ewes throughout the year, and construct seasonal time budgets. We used these data to examine whether bighorn ewes altered time budgets in response to seasonal changes in forage, day-length, and environmental variables. In addition, activity-time budgets were used to construct models of energy expenditure and intake (Chapter 4).

Due to its isolation in the heart of the largest wilderness in the lower 48 states, the study population is relatively undisturbed by modern development or agriculture. Only the older male segment of the population is hunted (6 permits/year). Therefore, the activity data provides a useful baseline for studies of other bighorn populations in areas more impacted by human developments and habitat changes.

STUDY AREA

Big Creek flows predominantly west to east and drains into the Middle Fork of the Salmon River. Elevations within the drainage range from 1067 m to 2896 m, and contain some of the greatest relief in Idaho. Southern exposures comprise the majority of the terrain on the north side of Big Creek. This area serves as important winter range to bighorn sheep, mule deer (Odocoileus hemionus), and elk (Cervus elaphus). Snow depths generally are low and southern aspects usually remain snow-free for much of the winter. The greater winter range extends for 48 km along the lower portion of the drainage. However, bighorn sheep occupy mainly the lower 19 km of the winter range.

Topography at lower elevations is characterized by steep V-shaped canyons. Abrupt changes in aspect result in markedly different plant associations. Southern exposures at lower elevations, where soil development is adequate, are dominated by grasslands. Soils are formed from granitic Idaho batholith parent material (Claar 1973), and are generally shallow and rocky. Numerous rock outcrops, cliffs, and talus slopes are present.

Bluebunch wheatgrass (Pseudoroegnenia spicata), Idaho fescue (Festuca idahoensis), junegrass (Koeleria cristata), needle and thread grass (Hesperochloa comata), Sandberg's bluegrass (Poa sandbergii), and cheat grass (Bromus tectorum) comprise the majority of graminoid biomass. Big sagebrush (Artemesia tridentata), rabbitbrush (Erecaneria nauseose), and bitterbrush (Purshia tridentata) are important shrub species associated with grasslands. Curl-leaf mountain mahogany (Cercocarpus ledifolius) forms extensive stands on steep rocky outcrops. Arrowleaf balsamroot (Balsamorhiza sagittata), western yarrow (Achillea millefolium), and lupine (Lupinus spp.) are important forbs. Douglas-fir forests are encountered on north aspects and ridgetops. Small stands and individual Douglas-fir also are scattered throughout the grasslands. All scientific names follow the National Plant Data Base, U. S. Department of Agriculture (http://plants.usda.gov/plants).

Summers typically were hot and dry with July and August usually having the highest average temperatures. Typically, maximum daily July temperatures averaged 35 C. Temperature patterns were relatively consistent from year to year. However, September 1994 was unusually warm and dry, and produced average daily temperatures higher than those reported in August. Moisture patterns were more variable than temperature patterns.

Total annual precipitation was 31.3, 53.8, 39.4, and 43.1 cm from 1994 to 1997 (National Weather Service, respectively). Over the long-term, annual precipitation has averaged 38.1 cm at Taylor Ranch in Big Creek. August and September typically were the months receiving the least precipitation. The remainder of annual precipitation occurred during winter in the form of snow or spring rain. Winter snowfall varied substantially from winter to winter. Snowfall during the months of November - February totaled 37.3 cm during the winter of 1994-95, 93.7 cm during 1995-96, and 84.8 cm during 1996-97.

METHODS

Remote Telemetry

Radio-telemetry employing motion-sensitive collars has been used to obtain activity budgets for non-habituated or cryptic animals. Studied ruminants have included elk (Craighead et al. 1973, Green and Bear 1990), white-tailed deer (Odocoileus virginianus; Kammermeyer and Marchinton 1977), and desert bighorn sheep (Ovis canadensis mexicana; Alderman et al. 1989). An observer needed to actively monitor and record data in the above studies. Consequently, radio-telemetry methods allowing automated remote collection of activity data were developed. These remote methods offered certain advantages: animals were observed continuously for a greater length of time, nocturnal behavior was monitored consistently, and more than one animal could be monitored continuously (Georgii 1981). The observers needed only to periodically maintain the equipment, therefore, their presence was less likely to alter animal behavior.

Automated remote telemetry systems were used to study red deer (Cervus elaphus L.) in Germany (Georgii 1981), moose (Alces alces) in Alaska (Risenhoover 1986; Miquelle 1990, 1992; MacCracken 1992), mule deer in California (Kie et al. 1991), black-tailed deer

(O. hemionus columbianus) in British Columbia (Gillingham and Bunnell 1985), and white-tailed deer in Michigan (Beier and McCullough 1988).

System Description.--

Nine ewes were captured using a dart gun and collared with Telonics radio-transmitters containing motion-sensitive tip switches. Signals were received from radio-collared animals by a Telonics TR-2 receiver using a Telonics RA-10 Omni-directional antenna , relayed to a Telonics TDP-2 digital processor, and recorded on a Gulton Rustrak (Manchester, New Hampshire) dual-channel strip-chart recorder. Three systems were placed in separate 30 gallon plastic coolers for protection. Coolers were strategically located on ridge tops that offered the best signal reception. Chart speed was set at 12.7 cm/hr (5 inches/hour).

Chart Interpretation.--

During operation, two lines were recorded: one for signal strength and one for motion/behavior changes. Motion/behavior lines reflected changes in pulse rate that were determined by the animal's head position. A lowered head position produced a faster pulse rate than a raised position. Different behaviors recorded different patterns on the strip chart. Experience in chart interpretation was obtained by simultaneously observing the behavior of transmitting ewes while watching data record on the strip chart. Knowledge of variations in signal strength aided interpretation of the pulse rate line. Both beginning and ending times were marked on the chart paper, and intermediate times also were marked whenever a unit was checked. Upon retrieving a chart, the interpreter placed tick marks at changes in behavior, and then measured the distance between changes. The length of time an animal engaged in an identified behavior was calculated by multiplying the distance by the time/distance ratio. Focal animals were monitored continuously for a maximum of 6 days, the length of time between battery and chart paper changes. If possible, monitored animals were selected randomly; however, frequently only a single individual produced a strong signal due to rugged topography or distance reducing the signal reception of other ewes. In such circumstances the bighorn ewe producing the strongest signal was monitored.

The validity of activity data collected by remote means was questioned by Gillingham and Bunnell (1985). However, other authors have rated their system accuracy at > 90% (Vallenberghe and Miquelle 1990). Our system accuracy was dependent upon the degree of behavioral detail selected for sampling. The finer the behavioral detail desired, the less certain the estimates. We distinguished active from inactive behavior, and within the inactive category, separated bedded (lying with head up) from "sleeping" (lying with head down). Other behaviors within the above categories were measured by direct observation. The accuracy of remote telemetry data interpretation was checked by comparing strip-chart data to information recorded independently in field notes. Eighty-one individual observations from the strip-chart were selected randomly and the interpreted behavior verified by direct observations. Accuracy was expressed as the percentage of correct observations.

Direct Observations

Within active and inactive bouts bighorns engaged in several behaviors of importance that could not be discerned from the strip chart recordings. Therefore, randomly selected, active focal animals were observed with 16 x 80 power binoculars from 100 to 500 m distance, and their behaviors recorded for 15 min using a cassette recorder. Later the cassette was replayed and behaviors timed using a stopwatch. Times spent in each behavioral category were converted to percentages of the 15 min observation. Categories included feeding on grass or forbs at ground level, feeding on grass or forbs above ground level, browsing, pawing through snow or gravel, moving side-hill, moving uphill, moving downhill, moving while continuing to feed, chewing cropped vegetation with head erect, standing alert and/or alarmed, interacting socially, and other. Feeding was defined as actually biting vegetation. During an observation, individual movements and total distance moved were estimated in meters. During inactive bouts, times spent ruminating and sleeping were estimated by similar observations, except that up to 3 ewes were monitored simultaneously.

Environmental Variables

Hourly weather data were collected by an automated meteorological station located at the base of the winter range. Each hour the station recorded maximum wind speed, wind vector, average wind speed, temperature, humidity, solar energy, precipitation, and barometric pressure on a Campbell Scientific CR10 datalogger (Campbell Scientific; Logan, Ut.).

Data Analysis

Based upon the annual reproductive cycle of bighorn ewes and plant phenology a year was divided into 5 periods. Summer or Period 1 (1 June to 16 August) corresponded to peak lamb drop and lactation, and availability of early summer forage. Late summer-fall or Period 2 (17 August to 15 November) corresponded to decreased lactation, gradual senescence of most herbaceous forage, possible fall resprouting of some grass species, and beginning of fall weather. Winter or Period 3 (16 November to 15 February) corresponded to mid-winter conditions of frequent snowfall, relatively low temperatures, senescent forage, and mating. Late winter or Period 4 (16 February to 31 March) corresponded to approximately the second trimester of gestation, and earliest green-up of some grasses. Spring green-up or Period 5 (1 April to 31 May) corresponded to the third trimester of gestation, green-up of all forages, and eventually movement to lambing ranges.

For remote telemetry data a sample unit was defined as 24 hr of continuous data collection on a radio-collared ewe. Due to migrations, deaths, and an irregular capture schedule, it was impossible to use a balanced factorial design that included all animals to test for differences among animals and years. Therefore, these differences were examined with separate t-tests or 1-way analysis of variance (ANOVA). The null hypothesis that no period differences existed in mean minutes engaged in a behavioral category within a full 24 hr day was tested with multivariate analysis of variance (MANOVA). Also, mean minutes active, mean bout-length, and mean number of bouts within daylight, night, dusk, and dawn, were tested with separate MANOVA's with period as the main effect. Dusk and dawn were defined as 1 hr before and after morning and evening civil twilight. Civil twilight was defined by the U. S. Naval Observatory, Astronomical Applications Dept. as beginning or ending when the center of the sun was geometrically 6 degrees below the horizon. Separate univariate ANOVA's for each behavioral category, mean minutes active per day-part, bout-length, and number of bouts were conducted with period as the main effect. Means were separated with Duncan's multiple range test. A second ANOVA using random subsampling was conducted to produce balanced designs, because such designs were considered to be more robust to mild violations of the assumption of heterogeneity of variance (Kirk 1982). Homogeneity of variance was evaluated using Bartlett's test, and normality was examined with Shapiro-Wilk's tests and normal probability plots. The null hypotheses examined by ANOVA were also checked using a Kruskal-Wallis test and means separated using multiple

Mann-Whitney U tests (Fry 1993). Where necessary, percentages were arcsine transformed (Kirk 1982).

A graphical analysis of the mean number of minutes active during each hour of the day was conducted separately for each period. Direct observation data were analyzed using a G-factor test of homogeneity (Sokal and Rohlf 1981, Ott 1993). To meet statistical assumptions feeding and moving behaviors were combined into single categories, and the category "other" dropped from the analysis. This left feeding, pawing, moving, head-up chewing, stand alert, and socializing as the behavioral categories.

Distance moved each 24 hr period was estimated by randomly choosing individual distance movements from the direct observation data. These distances were averaged to produce an estimate of the average distance moved per movement. Then the number of movements per minute was estimated by counting all movements made in each direct observation period and dividing by time. Multiplying these 2 ratios together produced an estimate of the number of meters moved per active minute. This rate was then multiplied by the number of active minutes in a 24 hr period obtained from Rustrak recordings. The null hypothesis that no differences existed between periods in mean distance moved/24 hr was tested by ANOVA. Means were separated using Duncan's multiple range tests. Analysis of variance results were checked with Kruskal-Wallis tests using multiple Mann-Whitney U tests to examine differences between period means (Fry 1993).

A second method of estimating distance traveled/24 hr was used as a check. When possible, ewes were observed directly for an entire activity bout. The average distance moved/bout then was multiplied by the number of bouts determined from Rustrak recordings.

The estimates of distance moved during a 24 hr day obtained by the 2 methods were compared within periods using t-tests.

Moonlight's effect on the activity patterns of bighorn ewes was examined by regressing minutes active at night on the fraction of the moon illuminated obtained from tables supplied by the U. S. Naval Observatory. A simple linear regression was conducted for each period, and for the period July 14 to Oct. 11, 1994. This period was chosen because nights were known to be cloudless.

The effects of environmental variables on bighorn ewe behavior were assessed by developing a multiple regression model with minutes active each hour as the dependent variable and weather data serving as the independent variables. Stepwise selection as defined in the SAS/STAT Guide for Personal Computers (SAS Institute; Cary N. C. 1987) was used as the model selection method. Independent variables were examined for multicollinearity, and the dependent variable was examined for autocorrelation using the Durbin-Watson statistic. Each model-selection method was run an additional time with minutes active the previous hour as an additional independent variable (Myers 1990).

RESULTS

A total of 6,504 hours or 271 twenty-four hour days of activity data on 9 ewes were collected by remote telemetry from 1994 to 1997. Ewes frequently moved behind rock outcrops or across ridges interrupting signal reception. Fragments of data less than 24 hr were not included in the analysis. System accuracy was estimated to be 84%. Most errors in interpretation occurred because strip chart recorders plotted a straight line when head position failed to activate the mercury tip switch. Thus, behaviors where sheep held heads erect for relatively long periods, such as stand alert, moving, feeding on shrubs, or feeding uphill on steep slopes were occasionally misinterpreted as inactive-bedded behavior.

No significant differences existed among years or animals except during summer 1994. One adult ewe was more active than the other radio-collared ewes, this was also apparent from direct observation. However, by fall 1994, her activity patterns were no longer notably distinct.

The amount of time bighorn ewes spent in different behaviors (active, inactive, bedded, and "sleeping") during a 24 hr day differed among periods (MANOVA, Wilks' lambda $P = 0.019$). Ewes were significantly less active and spent more time bedded and inactive during winter than during other periods (ANOVA, $P = 0.001$). The amount of time ewes slept did not differ between periods (ANOVA, $P = 0.334$; Table 3.1). Results of the Kruskal-Wallis test produced similar findings ($P = 0.001$ for active, inactive, and bedded behaviors, $P = 0.334$ for "sleeping").

Ewe activity varied between periods when the 24 hr day was divided into daylight, night, dusk, and dawn (MANOVA, $P = 0.001$ Wilks' lambda; Table 3.2). Ewes spent more time active in daylight hours during summer and spring green-up, than during winter (ANOVA, $P = 0.001$). During dawn hours, ewes were most active during late summer-fall and late winter, and least active during winter and spring green-up (ANOVA, $P = 0.0145$). The amount of time ewes were active at night did not differ between periods (ANOVA, $P = 0.052$), although ewes tended to be more active at night during late winter. At dusk, ewe activity did not differ between periods (ANOVA, $P = 0.5870$; Table 3.2).

Average bout length differed between periods (MANOVA, Wilks' lambda = 0.011; Table 3.3) when the 24 hr day was divided into daylight, night, dusk and dawn. Night foraging bouts were longer in winter and late winter than during summer (ANOVA, P = 0.025). However, average bout length per 24 hr day did not differ between periods (P = 0.49 by Kruskall-Wallis; Table 3.3).

Average number of active bouts differed between periods (MANOVA, Wilks' lambda = 0.001; Table 3.4). During a 24 hr day, the number of active bouts were significantly lower during winter (ANOVA, P = 0.014; Table 3.4). Ewes tended to have fewer night feeding bouts during summer and spring green-up, when daylight was longest, and also during winter. However, during late winter ewes tended to increase the number of nocturnal feeding bouts. There was no period difference between mean number of bouts during dusk or dawn.

Ewe activity generally followed a bimodal pattern through a 24 hr day (Figures 3.1 - 3.5). However, during summer, ewes were more active throughout the day and the bimodal pattern, although present, was not as evident. During late summer-fall and winter, the first peak in activity occurred shortly after dawn, followed by a decline in activity at mid-day; then activity increased to a second peak before dusk. As day-length increased during late winter and spring green-up, ewes had several feeding bouts late in the day interspersed with bedding. During all periods, the majority of activity occurred during daylight hours. Generally, lowest levels of activity occurred immediately preceding the morning feeding bout, and following dusk activity peaks.

Within individual active bouts, frequencies of behaviors based on direct observation did not vary significantly among periods (G = 27.807, d. f. = 20). However, when these were considered separately there were biologically relevant differences (Table 3.5). During summer and late summer-fall, the percentage of time spent feeding during an activity bout was lower than at other times of the year, and the amount of time spent moving and at stand alert was highest. During winter the percentage of time spent feeding during an activity bout was highest and stand alert behavior diminished. Pawing for food was relatively high during late summer-fall and winter. During inactive-bedded periods ewes ruminated an average of 65% of the time. There was no significant difference between periods in the percentage of bedded time spent ruminating (ANOVA, $P = 0.41$).

Bighorn ewes when considered to be active covered an average of 6.011 m/move, and moved 1.1797 times/min, thus covering an average of 7.1 m/min, while active. Multiplying the conversion factor by the number of active min/24 hr day produced an average distance traveled per 24 hr day of 4804.3 m (SE = 296.6), 4494.0 m (SE = 269.9), 3558.0 m (SE = 178.2), 4722.0 m (SE = 177.7), and 4548.6 (SE = 186.8) for periods summer, late summer-fall, winter, late winter, and spring green-up, respectively. Ewes moved significantly less distance during period 3, midwinter (ANOVA, $P = 0.001$). Bighorn ewes traveled an average of 473.8 m/active bout. This conversion factor multiplied by the number of active bouts/24 hr also produced an estimate of meters traveled per 24 hr day. No significant differences between the 2 methods were found using t-tests ($P = 0.790$, 0.5612, 0.047, 0.478, 0.766 for periods 1,2,3,4, and 5 respectively, $N = 40$).

During late summer-fall, winter, late winter, and spring green-up, bighorn ewes were not significantly more active at night when a greater portion of the moon was visible. Ewes apparently were influenced by lunar phase during summer ($P = 0.001$, $R^2 = 0.497$; Fig. 3.6-3.10). Field notes and weather data were consulted and a period of time was chosen where little or no cloud cover was present at night. This time period corresponded to the summer drought in the Northern Rockies. This linear regression of minutes active at night on fraction of the moon illuminated also was not significant ($P = 0.178$; Fig. 3.11).

Hourly meteorological station data was matched to 3,355 hours of activity data collected by remote telemetry. Solar energy and average wind speed consistently produced higher F ratios, lowered mean square error the greatest, and contributed most to raising the coefficient of determination (R^2; Table 3.6). Mallow's C_p indicated that humidity also affected minutes active per hour. At the 0.15 level of significance, hourly mean wind vector, atmospheric pressure, and temperature were also included in the model, and precipitation and maximum wind speed were dropped using the stepwise selection method (Table 3. 6). The coefficient of determination equaled 0.1125, indicating that the environmental variables measured generally did not greatly influence the hourly activity patterns of resident bighorn ewes. The Durbin-Watson statistic indicated a degree of autocorrelation in the data. Myers (1990) suggested adding an additional regressor to the model consisting of the dependent variable (minutes active) from the previous time period to deal with autocorrelation. Adding this new variable raised R^2 to 0.36 using the stepwise selection method. Minutes active in the preceding hour, solar energy, and average wind speed were the 3 most important variables influencing ewe behavior using this approach.

DISCUSSION

Reduced bighorn ewe activity during winter was consistent with the well documented seasonal cycle of northern ruminant energy metabolism. Northern ruminants generally exhibited a lower basal metabolic rate during winter, compared to summer. Silver et al. (1969, 1971), Thompson et al. (1973), and Holter et al. (1975) observed fasting metabolic rates in white-tailed deer (*Odocoileus virginianus*) 50% higher in summer compared to winter. Similar reductions in winter metabolism were documented in caribou (*Rangifer tarandus*; McEwan and Whitehead 1970) and roe deer (*Capreolus capreolus*; Weiner 1977).

Chappel and Hudson (1978) measured the resting metabolic rate (RMR) of bighorn sheep from October to May using open circuit indirect calorimetry. Their captive bighorns also demonstrated seasonal changes in metabolism, with RMR's lowest in February and highest RMR's in May. The amplitude of change was greater than 40% (Chappel and Hudson 1980). California bighorns (O. c. californiana) in British Columbia spent fewer daylight minutes feeding during winter than at other seasons (Eccles 1983).

Winter body mass loss, and reduced activity and dry matter intake accompanied declines in metabolism for most wild ruminants (McEwan 1975). Declines in basal metabolism, voluntary restriction of food intake, and reduced activity have been considered adaptations for dealing with winter's period of decreased temperatures, less than optimum forage conditions, and increased snow depth (Parker et al. 1983). Several authors have suggested that ungulates reduce active time during winter to conserve energy because food is scarce or snow conditions impede foraging (Craighead et al. 1973; Moen 1976, 1978; Gates and Hudson 1979). However, Risenhoover (1986) argued that reduced forage quality and patterns of forage distribution also may cause ungulates to reduce activity levels. Winter forage generally is higher in fiber and less digestible, thus slowing passage rate, and requiring more rumination time to reduce particle size sufficiently to permit passage into the omasum (Van Soest 1982, Robbins 1993). Seasonal changes in ewe activity paralleled trends in the crude protein and energy content of important forage species (Chapter 2).

Total amount of time ewes spent bedded increased during winter, consequently, absolute amount of time spent ruminating increased. Moose in Alaska ruminated an average of 67% of time spent bedded in winter (Risenhoover 1986), consistent with 65% for ewes in Big Creek. The amount of time ewes rested their head on the ground while bedded constituted a relatively minor portion of inactive behavior. This behavior was termed "sleeping", but it was not known whether bighorn were actually asleep in a strict physiological sense. However, most ungulates spend relatively little time sleeping compared to other mammals (Meddis 1975).

Direct observation data indicated that during midwinter ewes increased the proportion of active time spent actually biting and chewing vegetation. Ewes evidently maximized the amount of nutrition obtained while active and minimized the proportion of time spent in behaviors that did not acquire food. During winter, movements not associated with acquiring food were uncommon for moose (Risenhoover 1986).

With the onset of spring and improved forage quality; ewes increased activity levels, reflecting an increase in metabolic rate and the increased nutritional requirements of advanced gestation for pregnant ewes. Bighorn sheep in Montana were active 773 min/24 hr day during summer (Belovsky and Slade 1986) compared to 677 min/24 hr day in Big Creek. Similar increases in activity and metabolic rate have been observed in red deer (Georgii 1981), moose (Risenhoover 1986, Regelin et al. 1985, Van Ballenberghe and Miquelle 1990), and white-tailed deer (Silver et al. 1969, 1971; Thompson et al. 1973; Holter et al. 1975). In general, ewes did not increase bout length, but increased forage intake by increasing the number of daily feeding bouts. With improved forage digestibility and consequent increased passage rates, ewes may have maintained gut fill by feeding more frequently. In British Columbia, captive bighorns averaged 5 diurnal activity peaks (Eccles 1978), where studies of wild bighorns averaged 2 to 3 daily activity peaks in summer (Davis 1938, Van Dyke 1978, Sayre and Seabloom 1994). Geist (1971) and Hoefs (1974) reported Stone's sheep (Ovis dalli stonei) and Dall's sheep (O. d. dalli), respectively, averaged 4 activity peaks during summer with fewer activity peaks during mid-winter.

During summer ewes increased the distance traveled per day compared to winter. Similarly, the percent of the hour that desert bighorns spent moving peaked during the summer season (Alderman et al. 1989). Warrick (1985) had earlier suggested that increased movement rates observed during warm seasons were driven by an increased selectivity for the most nutritious plants. Predator avoidance also may account for the increased distance traveled each day. Increased foraging during summer and fall may be necessary to prepare northern ruminants for the rigors of winter, making foraging an important activity, even though food may be highly abundant (Van Ballenberghe and Miquelle 1990).

Dividing the 24 hr day into daylight, night, dusk, and dawn showed that following parturition, ewes tended to be less active at night compared to winter or late winter. Ewes may have reduced nocturnal activity to protect lambs (Alderman et al. 1989). The small amount of nocturnal activity observed in summer could be attributed to the regular repositioning of ewes between beds (Sayre and Seabloom 1994, Woolf 1970). The duration of nocturnal activity bouts during winter and late winter suggested that actual feeding bouts occurred. Ruminants may need to feed nocturnally during seasons with shortened daylight, because periodic food intake is necessary to keep the digestive system operating (Balch 1955, Welch 1969). Red deer (Georgii 1981) and moose (Risenhoover 1986) were more active at night during late winter and early spring compared to summer. Bighorn ewe nocturnal activity patterns were not related to lunar phase, except during summer. The reasons lunar phase should influence activity during this period and not others were unclear. Small sample sizes during this period may account for an apparent relationship. Elk nocturnal activity patterns in Utah were not affected by lunar phases (Collins et al. 1978). Similar to ewes in Big Creek, bighorn ewes in North Dakota were more active at dusk than dawn (Sayre and Seabloom 1994).

Solar energy or sunlight was the primary environmental variable related to bighorn activity patterns. The majority of activity occurred during daylight. Bighorn sheep primarily rely on vision to detect predators (Geist 1971), and may have minimized the amount of activity during darkness.

Average wind speed was also related to ewe activity. Direct observations of bighorns on windy days indicated a heightened alertness or nervousness. Collins et al. (1978) noticed that elk were more nervous on windy days in Utah, however, Bowyer (1981) reported a lack of correlation between elk activity and wind speed, temperature, or humidity.

With the possible exception of humidity, the other environmental variables in the model made only minor contributions to an already modest $\underline{R}^2$. Humidity showed an inverse relationship with activity, which contrasted to desert bighorns in Arizona (Alderman et al. 1989), where humidity was positively correlated with activity. Desert bighorns reduced movement during periods of high temperature (Alderman et al. 1989, Simmons 1969, Welch 1969, McCutchen 1984, Krausman et al. 1985). However, Sayre and Seabloom (1994) reported that Rocky mountain bighorn ewes in North Dakota did not alter activity patterns significantly at temperatures > 23 C. However, Stemp (1983) demonstrated using heart-rate monitors that bighorn sheep were stressed physiologically by temperatures above or below the seasonal thermoneutral zone. At Big Creek a positive correlation existed between temperature and activity. However, temperature was the last variable entered into the model without the additional regressor (minutes active the preceeding time period), and was dropped from the model once this regressor was added. Bighorn ewes in Big Creek responded to high temperatures by seeking shade, similar to ewes in North Dakota (Sarye and Sealbloom 1994). The physiological stress of high or low temperatures as indicated by increased heart-rates, panting, shade- and shelter-seeking, and postural adjustments may not be reflected in activity patterns recorded by changes in head position.

In summary, sunlight and gusty winds were the 2 environmental variables that mainly affected bighorn ewe activity patterns. Other variables, such as temperature, humidity, atmospheric pressure, precipitation, and wind direction, did not greatly influence bighorn ewe activity. Rocky Mountain bighorns may adjust their daily feeding and ruminating cycles to optimally fit seasonal forage conditions. Possibly, the physiological state and reproductive condition of bighorn ewes, as well as their social interactions, may produce greater influences on activity patterns, and thus obscure the effects of environmental variables on an hourly scale.

MANAGEMENT IMPLICATIONS

Activity patterns of bighorn ewes can be interpreted on annual and daily temporal scales. Annually ewes adapt to the stress of winter by reducing activity levels. Consequently, human disturbances that force ewes to increase their activity levels during midwinter may increase energy requirements at a time when ewes may be operating at a negative energy balance. Likewise, following parturition nursing ewes are faced with the energetic demands of lactation, possibly before they have completely recovered from winter. They appear to seek the most nutritious grasses and forbs. Human disturbance should also be limited at this time of year to avoid stressing lactating ewes and preventing access to important nutritional sources.

Ewes were the least active shortly before daylight, and after the morning and evening feeding bouts. Since ewes typically bed in or near escape terrain, human disturbances may have less impact during these hours. Mid-day, when ewes bed following the morning feeding bout, would be the most appropriate time to allow human disturbance. Aerial censuses scheduled opposite bedded periods may observe ewes while they are usually foraging in more open areas.

If bighorns adopt feeding-ruminating cycles that optimally fit seasonal forage conditions, then disturbances may disrupt these patterns. Bighorn ewes must have evolved to deal with occasional disruptions. However, if frequent disturbances prevent ewes from following adaptive feeding-ruminating cycles, then ewes may decline in body condition over time. Repeated disturbances may lower survival and fecundity, even though the tangible effects may be delayed to future seasons. Managers should allow bighorns a chance to recover from periods of repeated disturbance.

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Table 3.1 Average minutes/24 hour day bighorn ewes engaged in active, inactive, bedded, and sleeping behaviors from 1994-1997 at Big Creek, Idaho. Bedded and sleeping are subcategories of inactive behavior.

Period[a]	Active	SE	Inactive	SE	Bedded	SE	Sleeping	SE
Summer	677.5A[b]	41.8	762.5A	41.8	732.7A	42.4	23.5A	3.8
Late summer-fall	633.8A	38.1	806.3A	38.1	790.4A	37.0	21.5A	7.2
Winter	501.8B	25.1	938.3B	25.1	918.1B	27.4	15.1A	4.9
Late winter	665.9A	25.1	774.1A	25.1	744.0A	23.0	26.0A	6.8
Spring green-up	641.5A	26.3	798.6A	26.3	733.8A	26.7	17.4A	4.4

[a] Summer = 1 June to 15 Aug., Late summer-fall = 16 Aug. to 15 Nov., Winter = 16 Nov. to 15 Feb., Late winter = 16 Feb. to 31 March, Spring green-up = 1 April to 31 May.

[b] Means followed by the same letter within columns are not different (ANOVA, $\alpha = 0.05$).

Table 3.2 Average minutes bighorn ewes were active during daylight, night, dusk, and dawn at Big Creek, Idaho 1994-1997.

Period[a]	Daylight	SE	Night	SE	Dusk	SE	Dawn	SE
Summer	528.6A[b]	27.9	47.7A	10.4	61.9A	9.5	39.4A	7.8
Late summer-fall	416.8B	31.6	85.6A	19.6	60.2A	8.9	55.0AB	7.2
Winter	333.6C	15.3	93.3A	17.6	64.8A	8.9	22.3AC	5.2
Late winter	434.2B	24.4	122.0A	23.7	60.0A	9.3	49.6ABD	9.4
Spring green-up	481.6AB	23.2	54.5A	11.1	78.1A	8.2	29.7ACD	7.2

[a] Summer = 1 June to 15 Aug., Late summer-fall = 16 Aug. to 15 Nov., Winter = 16 Nov. to 15 Feb., Late winter = 16 Feb. to 31 March, Spring green-up = 1 April to 31 May.

[b] Means followed by the same letter within columns are not different (ANOVA, $\alpha = 0.05$).

Table 3.3 Average activity bout length (min/day) of bighorn ewes from Big Creek, Idaho 1994-1997.

Period[a]	Full day	SE	Daylight	SE	Night	SE	Dusk	SE	Dawn	SE
Summer	87.8A[b]	10.9	95.0A	9.1	15.5A	4.0	58.7A	9.8	35.9A	7.8
Late summer-fall	77.1A	7.4	101.1A	12.5	23.7AC	6.2	53.0A	9.4	52.3A	7.3
Winter	91.1A	8.6	93.9A	9.9	52.2BC	11.8	61.7A	8.9	22.6A	5.2
Late winter	91.6A	11.4	129.1A	9.9	32.5BC	4.8	47.1A	8.8	42.8A	9.2
Spring green-up	112.5A	14.0	108.3A	11.6	26.1AC	5.3	71.6A	8.5	26.8A	6.4

[a] Summer = 1 June to 15 Aug., Late summer-fall = 16 Aug. to 15 Nov., Winter = 16 Nov. to 15 Feb., Late winter = 16 Feb. to 31 March, Spring green-up = 1 April to 31 May.

[b] Means followed by the same letter within columns are not different (ANOVA, $\alpha = 0.05$).

Table 3.4 Average number of activity bouts/day for bighorn ewes in Big Creek, Idaho 1994-1997.

Period[a]	Full day	SE	Daylight	SE	Night	SE	Dusk	SE	Dawn	SE
Summer	9.8A[b]	1.1	6.3A	0.5	2.8ABC	0.6	1.0A	0.2	1.0A	0.2
Late summer-fall	9.0A	1.1	4.7B	0.3	3.4ABC	0.5	1.3A	0.2	1.0A	0.1
Winter	6.2B	0.5	4.2B	0.3	1.8AC	0.3	0.9A	0.1	0.7A	0.1
Late winter	9.2A	1.0	4.4B	0.4	3.7ABC	0.5	1.3A	0.2	1.3A	0.2
Spring green-up	7.2A	0.7	5.2A	0.4	2.2AB	0.4	1.1A	0.1	0.8A	0.1

[a] Summer = 1 June to 15 Aug., Late summer-fall = 16 Aug. to 15 Nov., Winter = 16 Nov. to 15 Feb., Late winter = 16 Feb. to 31 March, Spring green-up = 1 April to 31 May.

[b] Means followed by the same letter within columns are not different (ANOVA, $\alpha = 0.05$).

Table 3.5 Percentage of time bighorn ewes engaged in behaviors while active, determined by direct observation in Big Creek, Idaho 1994-1997.

Period[a]	Feeding[b]	Pawing	Moving	Head-up chewing	Stand Alert	Socializing
Summer	42.18	0.15	17.92	13.13	25.12	1.33
Late summer-fall	49.12	2.68	10.40	15.49	21.15	2.07
Winter	60.45	1.90	8.68	16.64	11.30	0.65
Late winter	49.50	0.60	14.29	22.62	12.13	0.78
Spring green-up	59.00	0.50	14.29	6.14	19.43	1.14

[a] Summer = 1 June to 15 Aug., Late summer-fall = 16 Aug. to 15 Nov., Winter = 16 Nov. to 15 Feb., Late winter = 16 Feb. to 31 March, Spring green-up = 1 April to 31 May.

[b] Feeding is defined as actually biting vegetation.

Table 3.6 Environmental variables[a] affecting bighorn ewe hourly activity in Big Creek, Idaho (1994-1997) as determined by stepwise multiple regression[b].

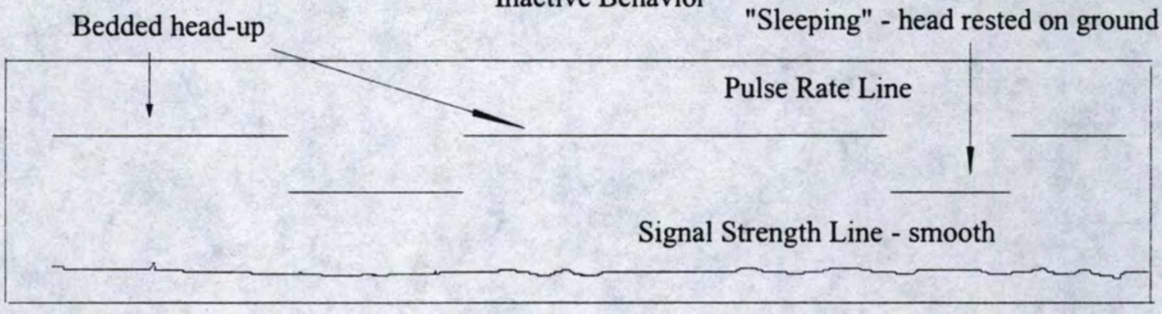
Step Variable	Partial $\underline{R}^2$	Model $\underline{R}^2$	Model C(p)	Parameter $\underline{F}$	Parameter Prob > $\underline{F}$
1 Solar energy	0.0826	0.0826	109.1235	301.9302	0.0001
2 Mean wind speed	0.0210	0.1036	39.9080	78.5382	0.0001
3 Humidity	0.0043	0.1079	17.6319	16.2102	0.0001
4 Wind vector	0.0026	0.1105	9.8409	9.7768	0.0018
5 Pressure	0.0008	0.1113	8.8355	3.0029	0.0832
6 Temperature	0.0012	0.1125	6.3250	4.5114	0.0337

[a] Solar energy (kW/m^2), mean wind speed (m/s), relative humidity (%), wind vector (azimuth), barometric pressure (mbars), temperature (C).

[b] Significance level for entry into the model = 0.15.

Figure 3.1 Example of Bighorn Ewe Acitivity Recorded on Gulton Rustrak Strip Chart from Big Creek, Idaho 1994-1997

Inactive Behavior



Active Behavior

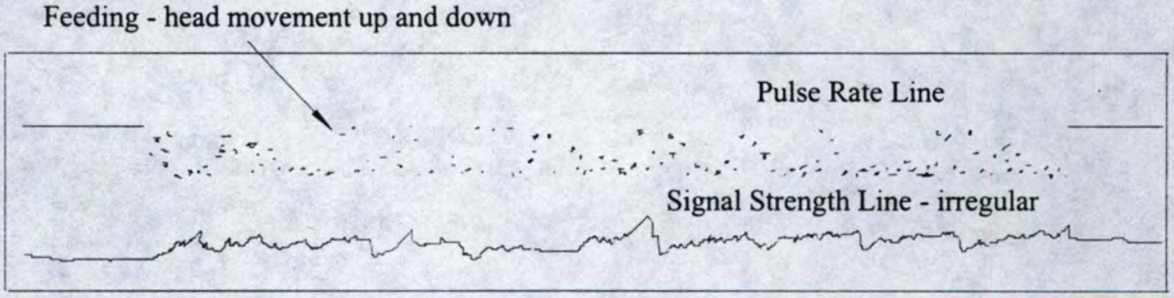


Figure 3.2 Summer (June 1- Aug. 15) average minutes active each hour for bighorn ewes from Big Creek, Idaho 1994-97

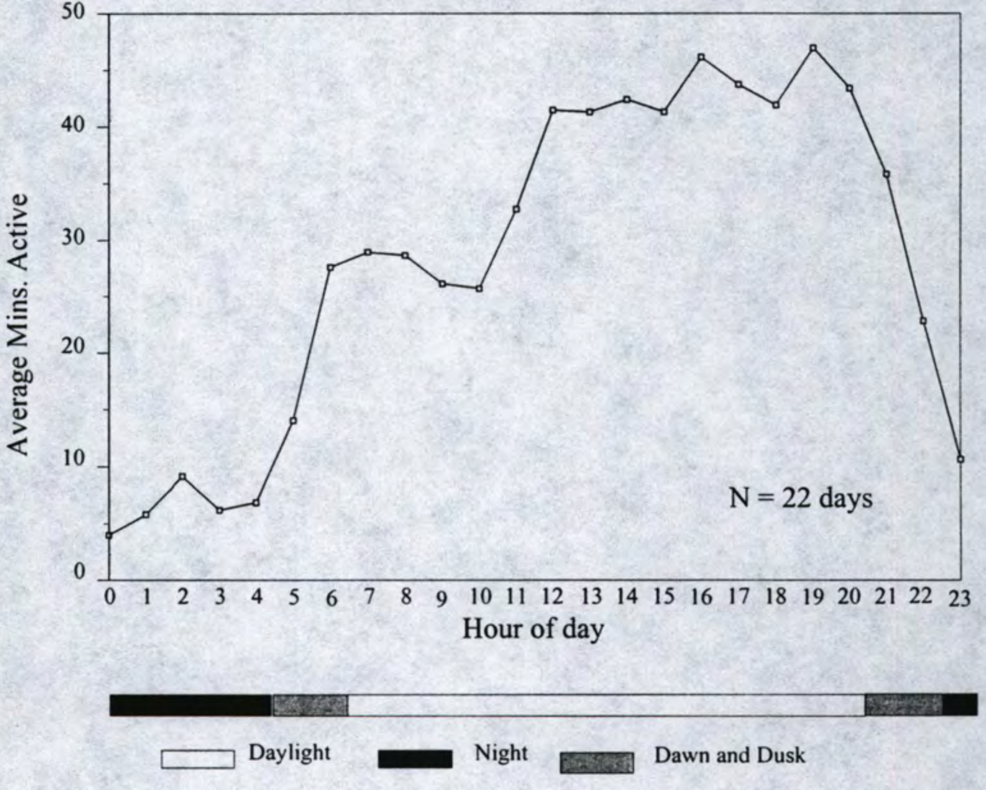


Figure 3.3 Late summer-fall (Aug. 16 - Nov. 30) average minutes active each hour for bighorn ewes from Big Creek, Idaho 1994-97

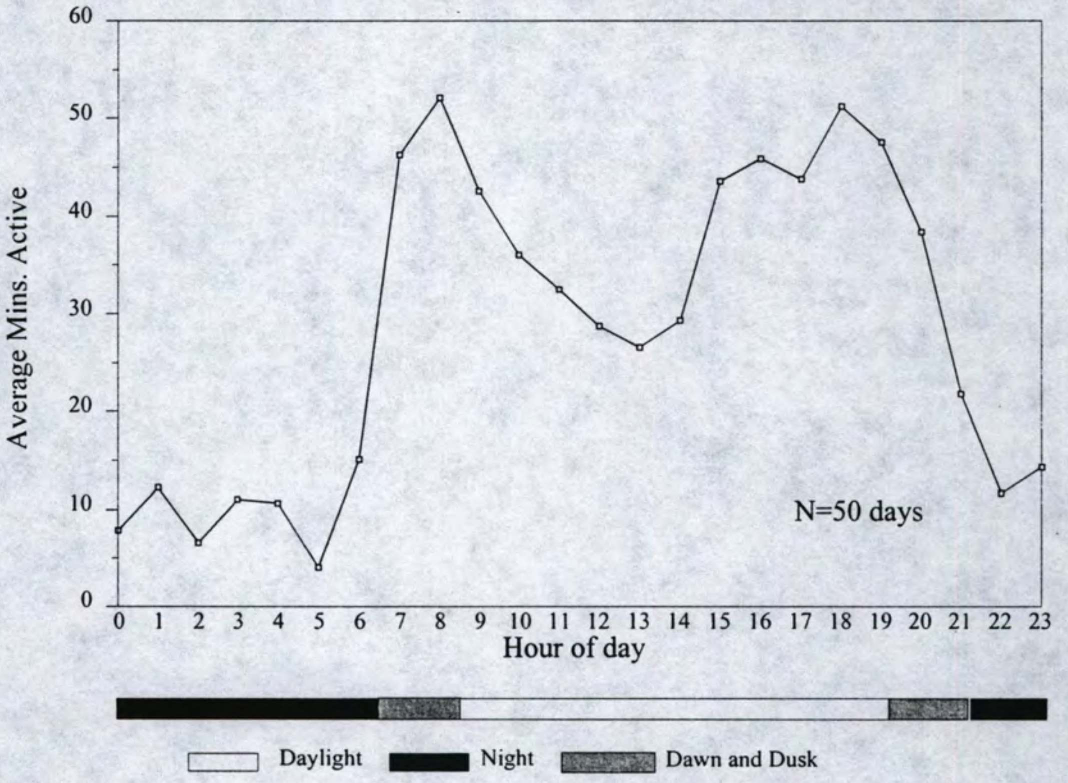


Figure 3.4 Winter (Dec. 1 - Feb. 15) average minutes active each hour for bighorn ewes from Big Creek, Idaho 1994-97

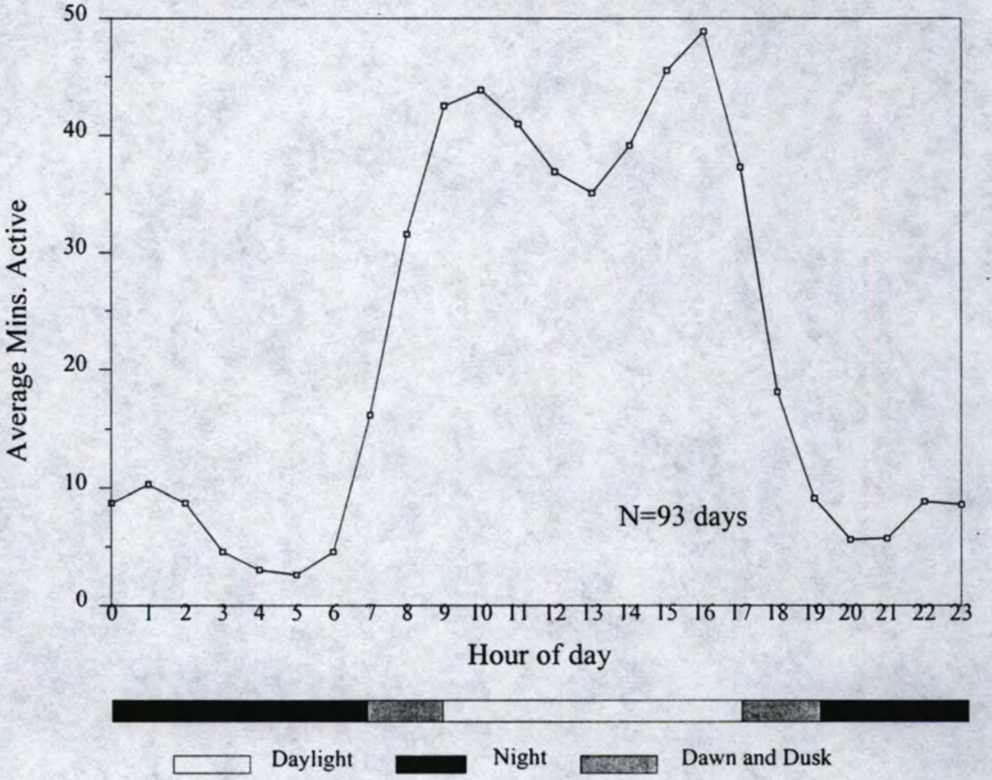


Figure 3.5 Late winter (Feb. 16 - March 31) average minutes active each hour for bighorn ewes from Big Creek, Idaho 1994-97

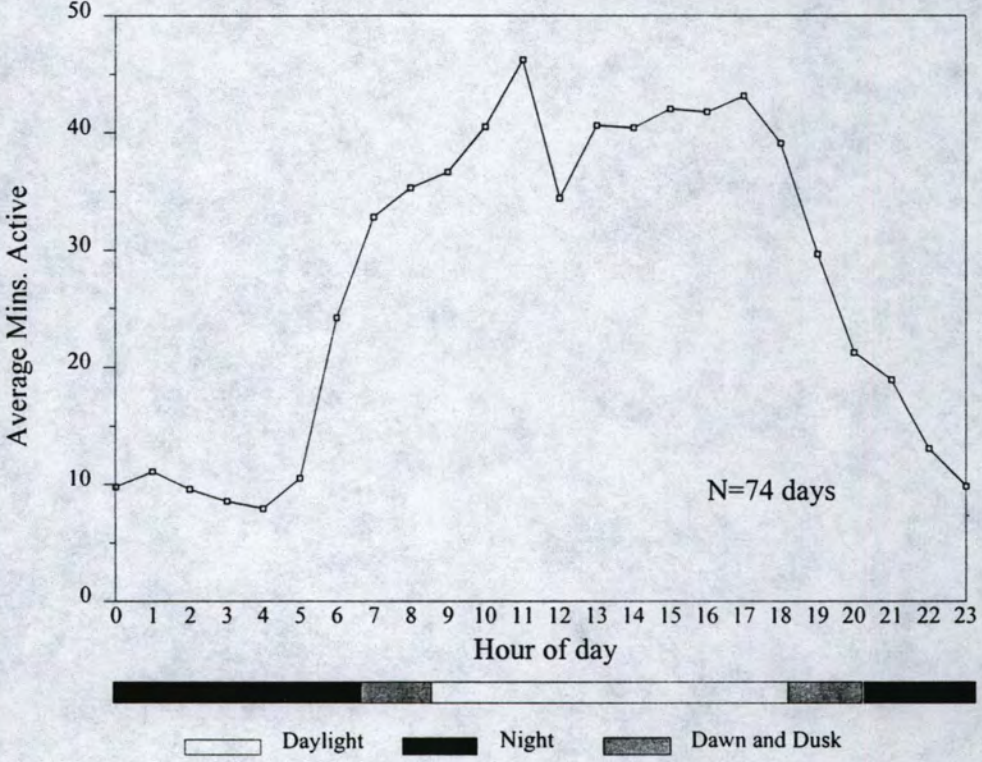


Figure 3.6 Spring green-up (April 1 - May 31) average minutes active each hour for bighorn ewes from Big Creek, Idaho 1994-97

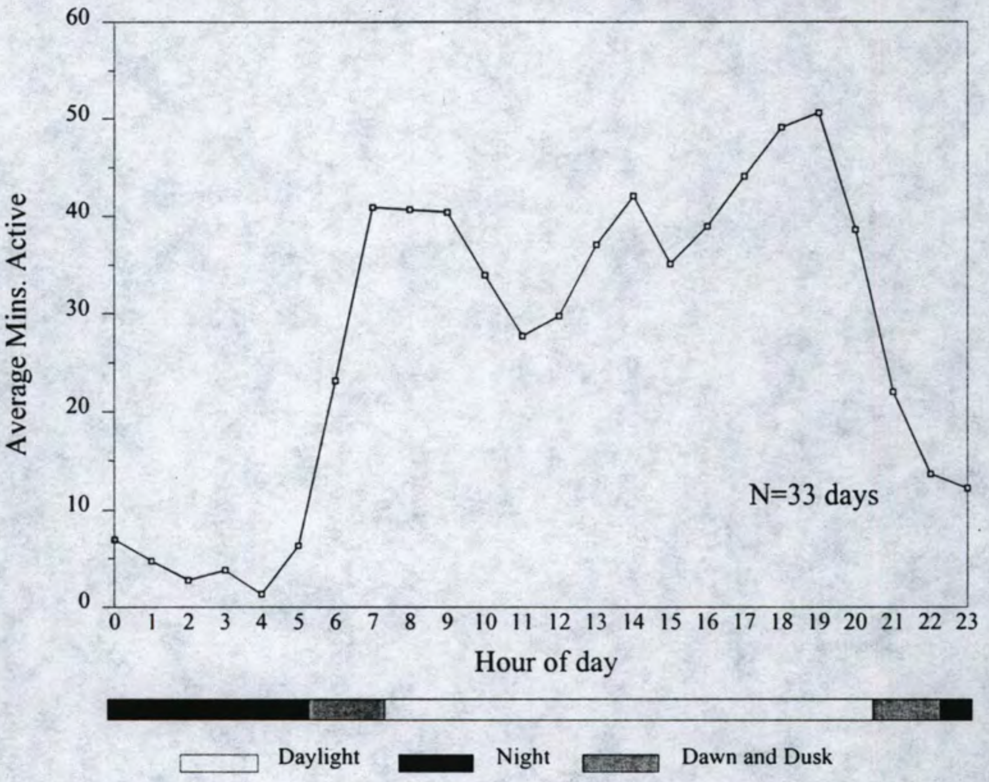


Figure 3.7 Summer (June 1 to Aug. 15) night activity predicted by fraction of moon illuminated for bighorn ewes from Big Creek, Idaho 1994-97

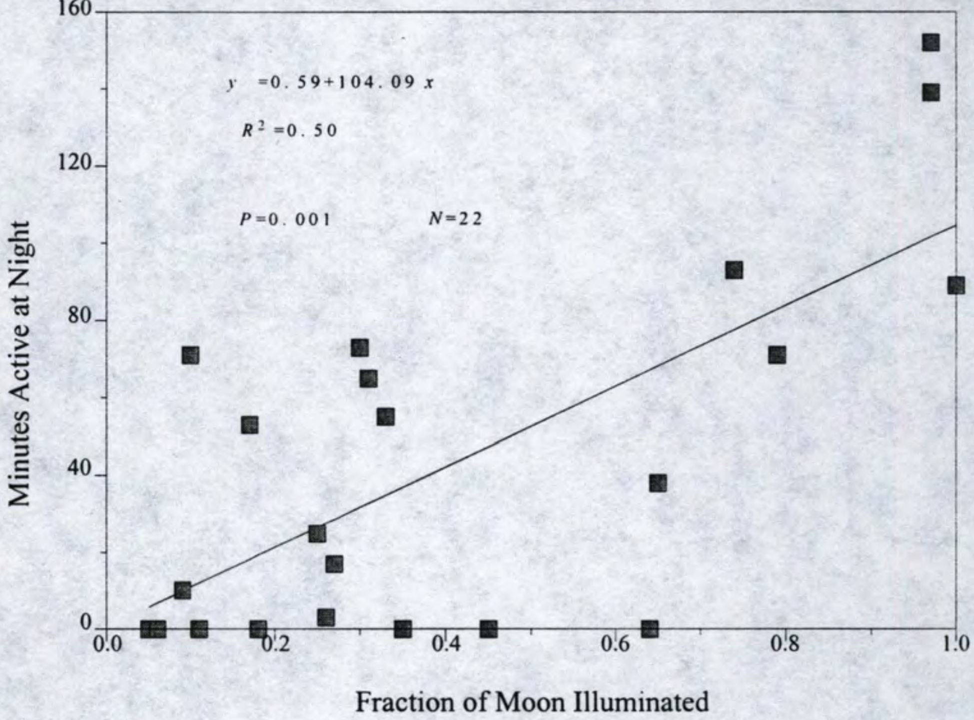


Figure 3.8 Late summer-fall (Aug. 16 to Nov. 30) night activity predicted by fraction of moon illuminated for bighorn ewes from Big Creek, Idaho 1994-97

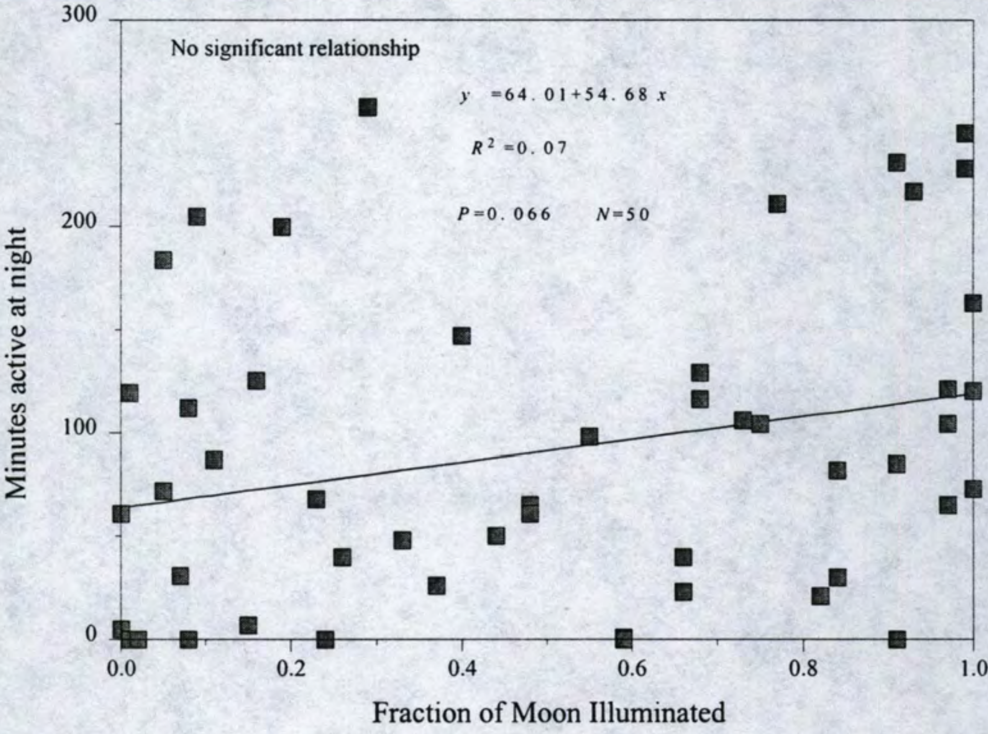


Figure 3.9 Winter (Dec. 1 to Feb. 15) night activity predicted by fraction of moon illuminated for bighorn ewes from Big Creek, Idaho 1994-97

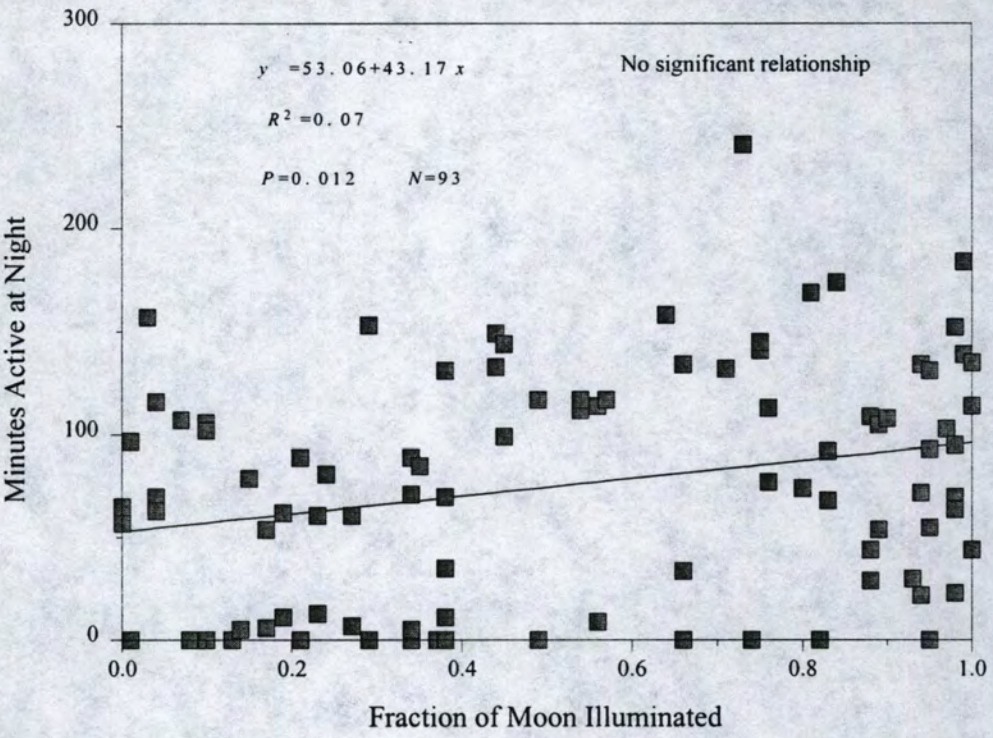


Figure 3.10 Late winter (Feb. 16 to March 31) night activity predicted by fraction of moon illuminated for bighorn ewes from Big Creek, Idaho 1994-97

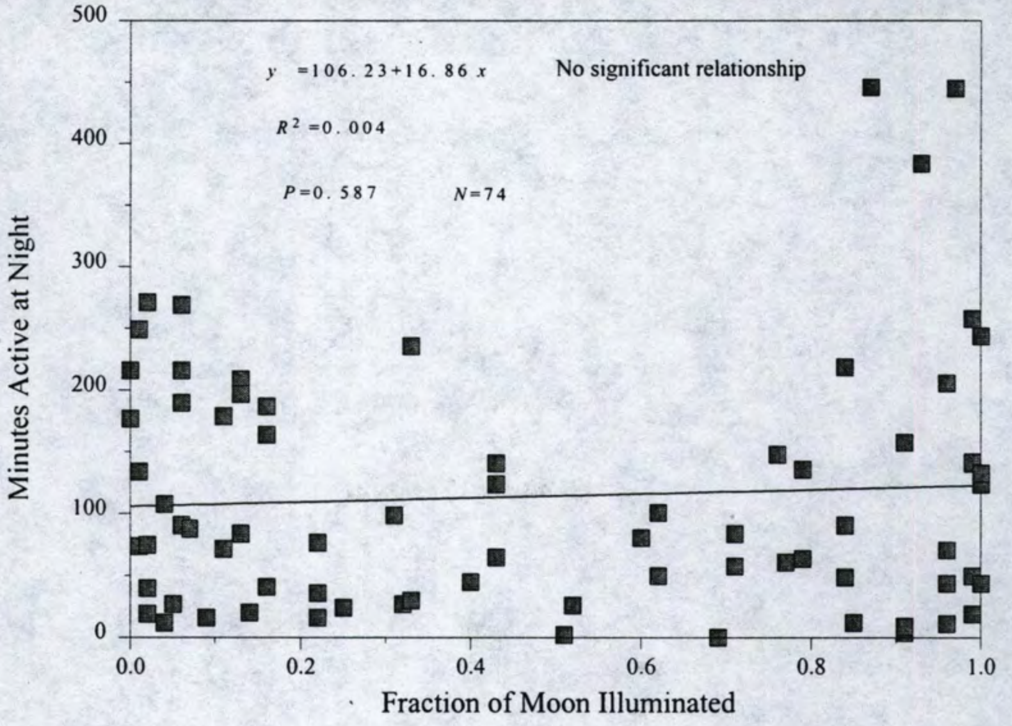


Figure 3.11 Spring green-up (April 1 to May 31) night activity predicted by fraction of moon illuminated for bighorn ewes in Big Creek, Idaho 1994-97

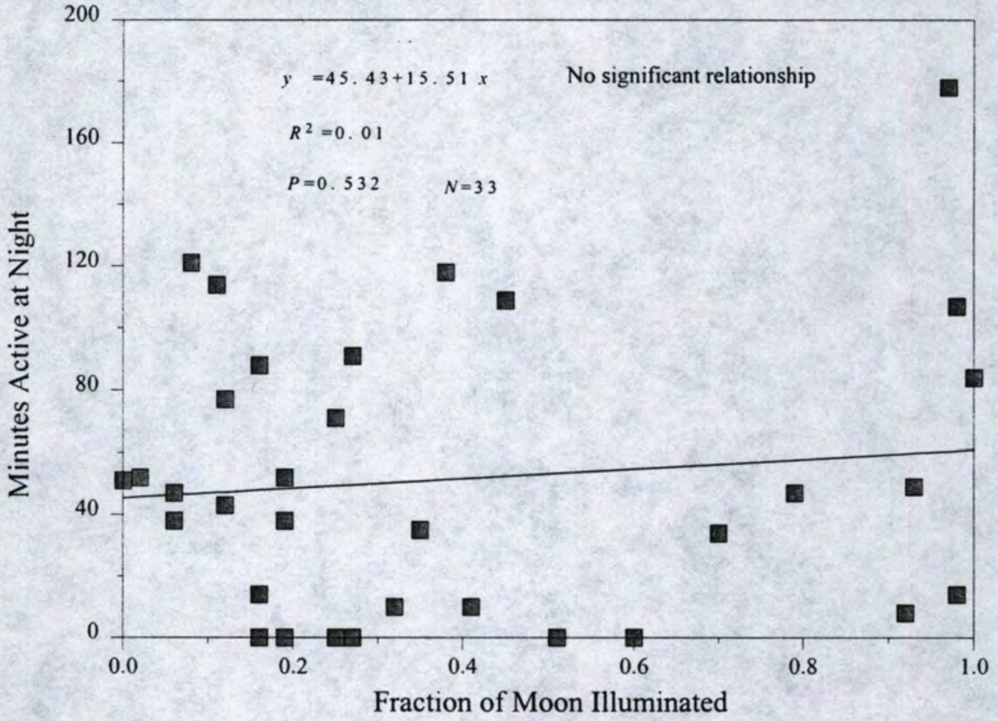
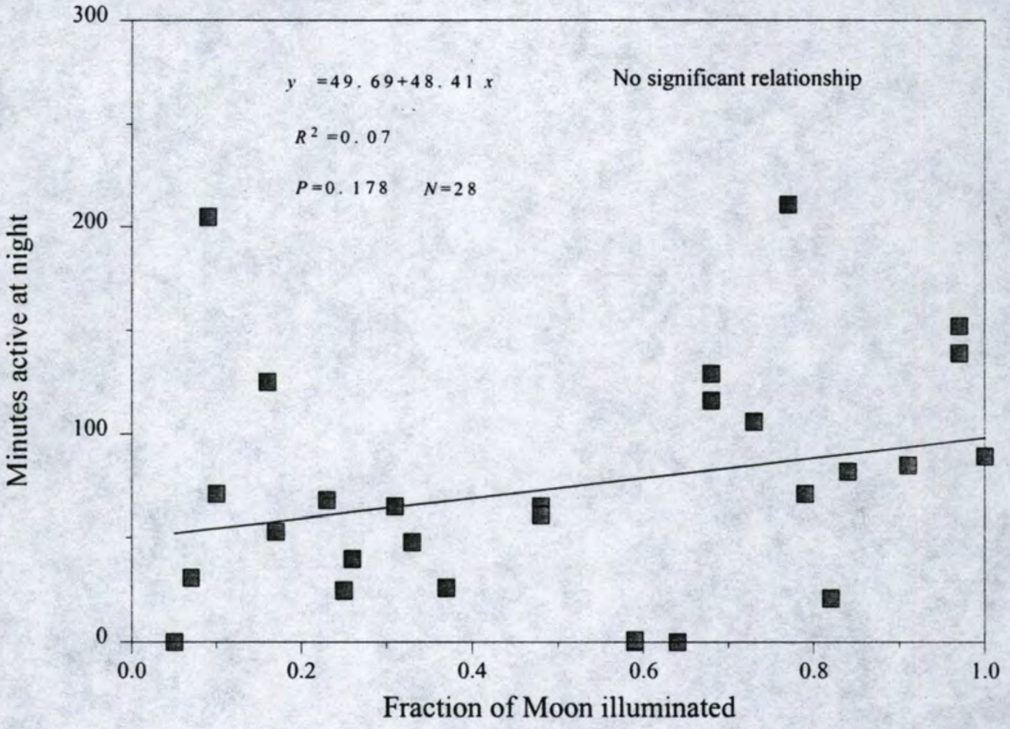


Figure 3.12 Minutes bighorn ewes were active at night predicted by fraction of moon illuminated at Big Creek, Idaho (July 14 to Oct.11, 1994)



Chapter 4

Modeling Energy Requirements and Intake of Bighorn Ewes in Central Idaho

INTRODUCTION

Bighorn sheep (Ovis canadensis canadensis) require energy to maintain basic cellular processes and to produce new tissue. Failing to obtain adequate energy intake decreases health, disease resistance, and reproductive potential, and may result in mortality. Furthermore, the bighorn's pursuit of nutrients affects their environment. Bighorns comprise one component of a suite of herbivores that interact dynamically with the resident plant community. Knowledge of energy requirements and intake of bighorn ewes will enable biologists to better understand the ecology of bighorn sheep in central Idaho.

Adult northern ungulates typically follow a seasonal cycle of weight change that reflects changes in forage quality and quantity (Wood et al. 1962, Renecker and Hudson 1986). Generally, individuals reduce activity and forage intake during winter, and may enter a period of negative energy balance during this season. Animals then catabolize fat and muscle to provide energy until spring green-up. Animals that enter winter in better condition survive and reproduce more successfully (Mautz 1978). Thus, the energy balance of bighorn sheep during spring, summer, and fall greatly influences their nutritional status during winter (Hebert 1973). Pregnant and lactating females must cope with the added energetic demands of these processes, and may not replenish energy reserves sufficiently to reproduce in consecutive years. Animals in poor condition also may be more susceptible to diseases.

Therefore, assessment of the nutritional status of bighorn ewes in terms of energy has a direct bearing on expected future population changes.

Carrying capacity continues to be a useful theoretical concept, but has proven difficult to calculate in practical applications (Macnab 1985). Much of the difficulty stems from a lack of specific information on nutritional requirements and nutrient intakes. Energy requirements and energy intakes for bighorn sheep in central Idaho have not been calculated. The calculation of these values is complex and dynamic, because availability of nutrients and the metabolism of bighorn ewes change seasonally. Therefore, based upon data collected in the Big Creek drainage of central Idaho from 1994 to 1997, we constructed 5 seasonal models to calculate: the energy requirements and energy intake of pregnant bighorn ewes. Our objectives were to assess the nutritional status of bighorn ewes in terms of energy, evaluate seasonal differences in energy balance (energy intake - energy expended), and illuminate which factors were most likely to cause negative energy balances.

STUDY AREA

Big Creek flows predominantly west to east and drains into the Middle Fork of the Salmon River. Elevations within the drainage range from 1067 m to 2896 m, and contain some of the greatest relief in Idaho. Southern exposures comprise the majority of the terrain on the north side of Big Creek. This area serves as important winter range to bighorn sheep, mule deer (Odocoileus hemionus), and elk (Cervus elaphus). Snow depths generally are low and southern aspects usually remain snow-free for much of the winter. The greater winter range extends for 48 km along the lower portion of the drainage. However, bighorn sheep occupy mainly the lower 19 km of the winter range.

Topography at lower elevations is characterized by steep V-shaped canyons. The highly dissected nature of the study area is reflected in the vegetation. Abrupt changes in aspect result in markedly different plant associations. Southern exposures at lower elevations, where soil development is adequate, are generally dominated by grasslands. Soils are formed from granitic Idaho batholith parent material (Claar 1973), and are generally shallow and rocky. Numerous rock outcrops, cliffs, and talus slopes are present.

Bluebunch wheatgrass (Pseudoroegnenia spicata), Idaho fescue (Festuca idahoensis), junegrass (Koeleria cristata), needle and thread grass (Hesperochloa comata), Sandberg's bluegrass (Poa sandbergii), and cheat grass (Bromus tectorum) comprise the majority of graminoid biomass. Big sagebrush (Artemesia tridentata), rabbitbrush (Erecaneria nauseose), and bitterbrush (Purshia tridentata) are important shrub species associated with grasslands. Curl-leaf mountain mahogany (Cercocarpus ledifolius) forms extensive stands on steep rocky outcrops. Arrowleaf balsamroot (Balsamorhiza sagittata), western yarrow (Achillea millefolium), and lupine (Lupinus spp.) are important forbs. In riparian areas Douglas-fir (Pseudotsuga menzesii), quaking aspen (Populus tremuloides), black cottonwood (Populus trichocarpa), red-osier dogwood (Cornus stolonifera), hawthorn (Crataegus douglasii), willow (Salix spp.), and thimbleberry (Rubus parviflorus) constitute major species. Douglas-fir forests are encountered on north aspects and ridgetops. Small stands and individual Douglas-fir are also scattered throughout the grasslands. All scientific names follow the National Plant Data Base, U. S. Department of Agriculture (http://plants.usda.gov/plants).

Summers were typically hot and dry with July and August usually having the highest average temperatures. Typically, maximum daily July temperatures averaged 35 C. Temperature patterns were relatively consistent from year to year. However, September

1994 was unusually warm and dry, and produced average daily temperatures higher than August's. Moisture patterns were more variable than temperature patterns. Total annual precipitation was 31.3, 53.8, 39.4, and 43.1 cm from 1994 to 1997 (National Weather Service, respectively). Over the long-term, annual precipitation has averaged 38.1 cm at Taylor Ranch in Big Creek. August and September were typically the months receiving the least precipitation. The remainder of annual precipitation occurred during winter in the form of snow or spring rain. Winter snowfall varied substantially between years. Snowfall during November through February equaled 37.3 cm during the winter of 1994-95, 93.7 cm during 1995-96, and 84.8 cm during 1996-97.

METHODS

A factorial model of daily energy requirements was developed using data obtained from remote telemetry recordings (Chapter 3), direct observations, meteorological data, and the literature. Parameter estimates were adjusted for each of 5 time periods to reflect seasonal changes in animal metabolism, activity patterns, weather, and plant phenology. Likewise, a companion model was developed to estimate daily energy intake based upon observed bite rates and sizes, diet composition (Chapter 2), forage nutritional analyses (Chapter 2), activity patterns, and values obtained from the literature. Results were calculated for each day for which 24 hr of activity data were available. Model results from both models could then be compared to assess the energy balance of resident bighorn ewes.

Energy Requirements

Total energy expenditure was divided into energy required for maintenance and productive processes, and each of these categories was further divided into its basic components. A component's energetic cost per unit time was obtained from the literature, and then multiplied by the component's estimated duration in the daily life of a bighorn ewe. Duration estimates were obtained from activity budgets developed from remote telemetry and direct observation data (Chapter 3). Component energy costs were then summed to furnish an estimate of total daily energy expenditure.

Since energetic costs, activity time budgets, and plant phenology vary seasonally, the year was divided into 5 seasons, or periods. Period 1, summer (1 June to 16 August), corresponded to peak lamb drop and lactation, and availability of summer forage. Period 2, late summer-fall (17 August to 15 November), corresponded to decreased lactation, gradual senescence of most herbaceous forage, possible fall resprouting of some grass species, and beginning of fall weather. Period 3, winter (16 November to 15 February), corresponded to mid-winter conditions of frequent snowfall, relatively low temperatures, senescent forage, and mating. Period 4, late-winter (16 February to 31 March), corresponded to approximately the second trimester of gestation, and earliest green-up of some grasses. Period 5, spring green-up (1 April to 31 May), corresponded to the third trimester of gestation, green-up of all forages, and eventually movement to lambing ranges.

Maintenance Energy Expenditure Parameters.--

Daily maintenance energy expenditures included the energy required to meet basal metabolism, activity, thermoregulation, and the heat increment of feeding (Robbins 1993). Basal metabolic rate (BMR) is defined as the energy expenditure of an animal in muscular and psychic repose, in a thermoneutral environment, and in a postabsorptive state (Brody 1945, Kleiber 1961). Since it is almost impossible to meet the requirements for obtaining a BMR, Chappel and Hudson (1980) reasoned that resting metabolic rate (RMR) was the appropriate base to which other energy costs should be added. Resting metabolic rate requires the measured animal be in a defined thermal and nutritional environment, and it contains the heat increment of feeding. Fasting metabolic rate (FMR) requires that the animal be fasted for a specified time period, but does not require the animal to be in a fully postabsorptive state.

Northern cervids have exhibited a well documented seasonal cycle of energy metabolism where BMR and RMR, are reduced during midwinter (McEwan 1975). Chappel and Hudson (1978a, 1978b) measured the RMR in bighorn sheep from October to May, and demonstrated that bighorn sheep also exhibited seasonal changes in metabolic rate. Rates were highest in May and lowest in February, with the oscillation's amplitude greater than 40%. Silver et al. (1969, 1971) observed FMR's in white-tailed deer (Odocoileus virginianus) over 50% higher in summer than in winter. Chappel and Hudson (1979) reported the RMR of a 72 kg bighorn ewe in January to be 69.54 kcal/kg$^{0.75}$/day while lying with head erect as measured by indirect calorimetry. To estimate RMR during summer or period 1, we increased this value by 50%, yielding an estimate of 104.31 kcal/kg$^{0.75}$/day or 0.07244 kcal/kg$^{0.75}$/min. Similarly, the RMR for periods 2 through 5 were adjusted to correspond to seasonal changes in metabolism. Percent changes were estimated from Chappel and Hudson (1978b, Figure 3, p. 396).

Bighorn ewes frequently rest their head on the ground while bedded. This behavior was defined as "sleeping" in Chapter 3, and was reliably recorded by remote telemetry. The energetic cost of lying with head down differed from head up by 12% in wapiti (Cervus elaphus; Pauls et al. 1981), and dozing moose (Alces alces) used 7% less energy than alert moose while lying (Renecker et al. 1983). Therefore, we reduced each period's estimate of RMR by 10% for time spent "sleeping". For example, for summer the RMR was reduced to 93.88 kcal/kg$^{0.75}$/day or 0.06519 kcal/kg$^{0.75}$/min, and this value multiplied by minutes spent "sleeping" per 24 hr.

While bedded, bighorn ewes ruminated an average of 65% of the time (Chapter 3). Rumination added an additional energetic cost of 2% above lying with head up for wapiti (Pauls et al. 1981) and moose (Renecker et al. 1983). For each period, we estimated rumination costs by increasing the RMR with head up by 2%. For summer, an estimate of 106.40 kcal/kg$^{0.75}$/day or 0.07389 kcal/kg$^{0.75}$/min was multiplied by minutes spent ruminating per 24 hr.

The energetic cost of standing was estimated as an increment above RMR while lying with head up. Chappel and Hudson (1979) reported an 18.9% incremental cost for standing, however, Dailey and Hobbs (1989) reported increments of 23 to 29%, and averaging 26%. We used Dailey and Hobbs' estimate of 26%, because they had a larger sample size. For summer, the estimated energetic cost of standing was 131.43 kcal/kg$^{0.75}$/day or 0.09127 kcal/kg$^{0.75}$/min. The RMR for Periods 2 through 5 were also increased by the 26% increment.

Chappel and Hudson (1978c) measured the incremental cost of feeding over standing using a metabolic crate and an open circuit respiratory pattern analyzer (Young et al. 1975). Ewes elevated their metabolism by 33.4% over standing. Measurements accounted for prehension and mastication, but did not include moving from plant to plant. We increased our estimate of the energetic cost of standing for each period by 33.4%, yielding an estimate of 175 kcal/kg$^{0.75}$/day or 0.12176 kcal/kg$^{0.75}$/min for the energetic cost of feeding for summer.

Bighorn ewes in Big Creek frequently pawed through gravel to obtain tubers of biscuitroot, arrowleaf balsamroot, and thistles; and through snow for grasses and forbs. Under certain conditions pawing most likely added an important energy cost to feeding. Fancy and White (1985) measured the energetic cost of cratering for caribou in snow. Values varied fourfold, and were dependent upon the density and hardness of the snow. The cost per limb movement was greater than walking, but the rate of movement was slower, making the rate of energy expenditure comparable to a slow walk. We calculated kcal/kg/km for a 72 kg ewe according to Taylor et al. (1982):

$$\text{kcal/kg/km} = 2.57 * BW^{-0.316}$$

where BW = body weight, and assumed a walking speed of 1km/hr to estimate the net cost of locomotion at 0.0323 kcal/kg$^{0.75}$/min. This value was added to the increment of standing over RMR for each period to estimate the energetic cost of pawing. For Period 1, summer, the energetic cost of pawing was 0.12357 kcal/kg$^{0.75}$/min.

Randomly selected, active focal animals were observed from a distance with high powered binoculars, and their behaviors were recorded for 15 min using a cassette recorder (Chapter 3). When sheep moved, the distance was estimated in meters, and whether the movement was side-hill, up-hill or down-hill was recorded. Distance moved each 24 hr was estimated by randomly choosing individual distance movements from the direct observation data. These distances were averaged to produce an estimate of the average distance moved per movement. Then, the number of movements per minute was estimated by counting all movements made in each direct observation period and dividing by the time. Multiplying these 2 ratios together produced an estimate of the number of meters moved per active minute. This conversion was then multiplied by the number of active minutes in a 24 hr period obtained from Rustrak recordings (Chapter 3). Finally, the estimated distance moved per 24 hr was multiplied by percent moved side-hill, up-hill, and down-hill. We modified the Parker et al. (1984) equation for energy expended for locomotion on level ground from:

$\text{kcal/kg/km} = 2.97 * BW^{-0.34}$ to:

$\text{kcal/kg}^{0.075}\text{/day} = (2.97 * BW^{-0.34} * D * BW)/BW^{0.75}$

where BW = body weight and D = distance to estimate energy expended traveling side-hill in terms of metabolic weight. The energetic cost of standing during the corresponding time period was added to energy expended for locomotion. Dailey and Hobbs (1989) measured the energetic cost of traveling uphill and downhill for bighorn sheep and mountain goat (Oreamnos americanus) using indirect calorimetry. Bighorn sheep expended 2.8 times the energy used on level ground to climb a 39% slope. Therefore, we increased the energetic cost of travel on level ground by this increment to estimate daily energy expended while traveling uphill. Dailey and Hobbs (1989) also measured energy expended or recovered moving down-hill on similar slopes. Some animals expended energy, while others actually recovered a small amount of energy. However, the majority used an average of 1.08 times the amount of energy expended while traveling on level ground. Consequently, we used this increment to estimate daily energy expended while traveling downhill.

No estimates of the energetic cost of social behavior existed in the literature for bighorn sheep. Resident bighorn ewes exhibited a range of social behaviors that varied in intensity from simple staring to actively fighting and playing. However, from an energetic standpoint we considered average social behavior to be costly, and estimated the cost of social behavior by increasing the cost of feeding by 0.01 kcal/kg$^{0.75}$/min for each period. This method yielded an estimate of 0.11727 kcal/kg$^{0.75}$/min for summer.

Energetic Costs of Thermoregulation Parameters.--

During hot weather bighorn ewes often were observed panting. Consequently, we inferred that bighorns expended energy to maintain homeostasis when temperatures exceeded their upper critical temperature. Sayre and Seabloom (1994) considered temperatures > 23 C to be outside the thermoneutral zone of bighorn sheep in North Dakota. Stemp (1983) considered the upper critical temperature for bighorn sheep in Alberta to range from 18 to 20 C. Whittow and Findlay (1968) estimated the thermal cost of panting for ox (Bos taurus) to be 11% above total daily energy costs. However, their measurements did not include locomotion or traveling. Therefore, we estimated energetic costs of thermal panting by summing all energetic costs (other than locomotion) and increasing the total by 11%. From weather records and meteorological station data we estimated the number of min/24 hr in which temperatures exceeded 23 C, and multiplied by the estimated cost of thermal panting, which was 0.05367 kcal/kg$^{0.75}$/min during summer. Thermal panting continued through mid-September and resumed in late spring.

Temperatures below an animal's lower critical temperature also require additional energy expenditure to maintain homeostasis. The thermoneutral zone for bighorn sheep in winter pelage ranges from 10 to -20 C (Chappel and Hudson 1978a). Metabolic rates rise sharply from -20 to -30 C. Wind speed has negligible effects on metabolic rates at temperatures above -18 C, however, below this temperature even low wind speeds cause measurable increases in metabolic rate.

We examined meteorological station data and weather records to identify winter time periods when temperatures and wind speeds produced conditions outside the thermoneutral zone of bighorn sheep. However, no recorded time periods met the criteria described by Chappel and Hudson (1978a), therefore, energetic costs of thermoregulation were not included in models developed for winter and late-winter (Periods 3 and 4, respectively).

Energetic Costs of Production Parameters.--

Energetic costs of production in wild ruminants include costs of tissue growth, gestation, and lactation. Production cost estimates can be obtained by determining the energy composition of the tissues or milk produced (Robbins 1993).

Energy costs of lactating females have ranged from 4 to 7 times BMR, or 65 to 215% higher than non-lactating females (Robbins et al. 1981; Sadleir 1982, 1984; Robbins 1993). No estimates of milk production existed specifically for bighorn sheep, and due to centuries of artificial selection, values for domestic sheep were unlikely to resemble those of a wild ungulate (Robbins 1993). Therefore, similar to Cook (1990), we used estimates of milk consumption for Columbia black-tailed deer (Odocoileus heminonus columbianus) fawns (Sadleir 1980) to derive estimates of bighorn lamb consumption. Black-tailed deer represented a wild ungulate close to bighorn sheep in body-size for which data existed.

First, we divided the mean weights of progressively older deer fawns into corresponding mean daily milk intakes to obtain estimates of g milk consumed/kg of body weight/day. Second, we used the regression equation from Blood et al. (1970):

$$Y = 4.57 + 0.173X$$

where Y = kg of body weight, and X = days post partum, to predict weights of bighorn lambs corresponding to the ages of the progressively older deer fawns. Then, we multiplied the estimated body weights by the estimates of milk consumed/kg body weight/day to obtain an estimate of g milk consumed/day. Chen et al. (1965) reported the gross composition of bighorn sheep milk, but did not furnish an estimate of energy content, however, Robbins (1993) reported the energy content of Dall's sheep (Ovis dalli dalli) milk as 1.48 kcal/g. We multiplied this conversion factor by estimates of g milk consumed/day to obtain an estimate of energy required for lactation at different lamb ages. We then developed a linear regression equation to predict energy required for lactation from days past parturition during Period 1 (1 to 76 days post partum) and period 2 through October 12, the last day suckling was observed (Table 4.1).

During periods 2 and 4, ewes experienced the added energetic cost of molting. We estimated hair weight using the equation from Robbins (1993, p 237):

$$\text{g of hair} = 0.035 * \text{BW}^{0.92}$$

where BW = body weight (g), assuming a 72 kg ewe. The energetic value of hair, approximately 5.3 kcal/g (Robbins 1993, p 237), was multiplied by hair weight (123.83 g), and the result divided by the number of days in each period to estimate the daily cost of pelage growth. Robbins (1993) reported hair grew at a relatively constant rate.

During winter, late-winter, and spring green-up pregnant ewes experienced the additional cost of gestation. Energetic costs of gestation follow a curvilinear function with the majority of fetal growth occurring in the third trimester (Robbins 1993). We used the equation for bighorn sheep from Robbins (1973, p 60):

$$\text{Log}_e\text{Y} = -1.2205 + 0.0325\text{X}$$

where Y = kcal/day and X = days since conception to calculate the daily energetic cost of gestation. We assumed Dec. 2 as the date of conception and 180 days as the gestation period (Wishart 1978).

Energy Requirement Model Development.--

Model inputs included minutes active, bedded, and sleeping per 24 hr day. In addition, days past parturition, and hours with average temperature > 23 C were inputs for summer and late-summer-fall. Plus, days since conception was an input for winter, late-winter, and spring green-up. Minutes active was partitioned into time spent feeding, standing, pawing, socializing, and moving as determined for each period. Time spent moving was further subdivided into time spent moving side hill, uphill, and downhill. Duration engaged in each behavioral category was multiplied by the energetic cost of each category as described above. The model was written in the MATLAB Version 5.0 language; (see Table 4.2 for an explanation of variables). Calculations for energetic costs of activity were as follows:

```
DAILY_FEED_COST = ACTIVE * PERCENT_ FEED * COST_FEED
DAILY_STAND_COST = ACTIVE * PERCENT_STAND * COST_STAND
DAILY_PAW_COST = ACTIVE * PERCENT_PAW * COST_PAW
DAILY_SOCIAL_COST = ACTIVE * PERCENT_SOCIAL * COST_PAW
MOVE_HORIZ_COST = (2.97 * 0.23362 * DISTANCE_HORIZ * 72) / 24.7121
MOVE_UP_COST = ((2.97 * 0.23362 * DISTANCE_UP * 72) / 24.7121) * 2.8
MOVE_DOWN_COST = ((2.97 * 0.23362 * DISTANCE_DOWN * 72) / 24.7121) *
        1.08
STAND_INCREM = TOTAL_TIME_MOVE * 0.08610
```

TOTAL_MOVE_COST = MOVE_HORIZ_COST + MOVE_UP_COST +
MOVE_DOWN_COST + STAND_INCREM .

Energy required during inactive bouts was partitioned into the costs of rumination, lying, and "sleeping". These costs were calculated in the model as follows:

DAILY_RUMIN_COST = BEDD * PROPOR_RUMIN * COST_RUMIN

DAILY_ LYING_COST = (BEDD - (BEDD * PROPOR_RUMIN) * COST_LYING

DAILY_SLEEP_COST = SLEEP * COST_SLEEP.

The energetic cost of lactation during period 1 was calculated by the regression equation:

LACTATION_COST = 53.3181 - 10.4655 * DAY_PAST_BIRTH.

The energetic cost of molting, DAILY_PELAGE_COST, was added on each day during summer and late-summer-fall. Likewise, the energetic cost of gestation was calculated by:

DAILY_GEST_COST = exp(-1.2205 + 0.0325 * DAY),

and added on each day during winter, late-winter, and spring green-up.

The energetic cost of thermoregulation during summer and late-summer-fall was calculated by the equation:

DAILEY_THERMO_COST = ((COST_RUMIN + COST_LYING + COST_SLEEP
+
COST_FEED + COST_STAND) * 0.11) * MINS_OVER_23C.

Energy Intake

We estimated daily energy intake from diet composition data determined from microhistological fecal analysis (Chapter 2), forage digestibility trials (Chapter 2), activity budgets (Chapter 3), observations of biting rates, estimates of bite sizes, and metabolizable and gross energy values obtained from the literature (Golley 1961, Robbins 1993).

Bite Rate Determination.--

Focal bighorn ewes were observed while foraging with 16x binoculars. Although we attempted to sample ewes randomly, focal ewes were normally chosen when visual conditions permitted the observer to accurately record separate bites on a plant species. While observing a foraging ewe, the observer recorded bite counts into a cassette recorder. Following the observation, the cassette was later replayed while being timed with a stop watch, the rate calculated, and recorded as bites/min for that species. Frequently, it was not possible to accurately determine the species, or ewes rapidly switched from one species to another. Under such circumstances the bite count was labeled "generic". Generic bite counts were necessarily used for small forbs and small grasses.

Bite Size Determination.--

Resident bighorn ewes fed upon some species and categories of vegetation differently. This fact necessitated the use of several methods to determine bite sizes. To determine bite sizes of bunch grasses and larger forbs, proper lighting, topography, vegetation, ewe behavior, and weather needed to coincide. Consequently, this type of data needed to be collected opportunistically. Ewes were observed feeding on an individual clump of bunch grass, and the number of bites were counted. Later, the individual clump was located and we estimated the amount of vegetation removed. Then, from a similar nearby clump of bunch grass we clipped an equivalent amount of vegetation, oven-dried the sample at 40 C for 48 hr, weighed the sample, and divided the total weight by the number of bites taken. Smaller forbs were very seldom visible from a distance, even with binoculars, therefore, it was necessary to assume ewes pulled the entire plant from the ground.

Browse species were fed upon by 3 different methods: 1) stripping leaves and bark off with their teeth, 2) biting off individual leaves, and 3) biting off twig ends. Ewes frequently browsed bitterbrush by stripping leaves, and bites were estimated by recording the strip lengths on a plant after a feeding observation. Bite sizes were then simulated by hand-stripping similar lengths on another plant. Ewes frequently fed upon species with larger leaves, such as elderberry, by biting off 1 or several leaves, and occasionally large clumps of leaves and berries. Ewes were observed while browsing with high powered binoculars, and the bite sizes estimated and recorded using a cassette recorder. Bite sizes were then later hand-simulated by obtaining similar bite sizes from fresh material. All samples were placed in individual paper bags, oven-dried at 40 C for 48 hr, and weighed.

Bighorn ewes also browsed by biting off the tips of twigs, especially curl-leaf mountain mahogany. We developed a regression equation to predict the amount of material removed from curl-leaf mountain mahogany shrubs. Representative twigs were clipped, and diameters measured at the point of browsing with calipers. Samples were then oven-dried, weighed, and dry weight regressed on diameter at point of browsing (Peek et al. 1971, MacCracken and Van Ballenberghe 1993). Twigs browsed by ewes could then be measured and bite sizes predicted from the regression equation:

$$\text{g of browse} = -0.0742 + 0.2505 * \text{mm at point of browsing.}$$

Intake Model Development.--

Metabolizable energy for each species that constituted ≥ 1 % of diet composition in at least 1 period was calculated by the equation:

BITE_RATE * BITE_SIZE * GE * DIGESTIBILITY * ME * DIET_COMP

where

BITE_RATE = bites/min determined from field observations of foraging ewes.

BITE_SIZE = g/bite determined from field observations and clipping, drying, and weighing hand-simulated bites.

GE = gross energy of grasses, forbs, and browse from Golley (1961).

DIGESTIBILITY = Apparent invitro digestible dry matter coefficients determined using forage samples collected from the study area (Chapter 2).

ME = apparent metabolizable energy coefficients: 81.8% for forbs, grasses, and sedges; 80.6% for shrubs and winter browse stems; and 76.4% for conifers (Robbins 1993:306).

DIET_COMP = % diet composition determined from microhistological fecal analysis (Chapter 2).

Variable values were determined for each species for each of the 5 periods to reflect seasonal changes in plant phenology and diet selection. Bighorn ewes consumed some species that were not collected for nutritional analysis. We dealt with this problem using methods similar to Leslie et al. (1984). We employed the following methods: (1) substituted nutritional compositions of closely related species from the same forage category; (2) employed linear and polynomial regression equations (Chapter 2) to predict nutrient content;

and (3) averaged values for all species within a forage category to estimate nutritional content of forages that could not be identified to genus or species. Similarly, bite-rates were not collected for each species identified in the diet. Consequently, we used bite-rates of species with similar morphology in the model, or relied upon "generic" bite-rates for that forage category.

The sum of metabolizable energy for all species, SUM_ME, was multiplied times the total amount of time spent biting vegetation, TIME_FEED (Chapter 3) to obtain an estimate of total daily energy intake. Additionally, energy intake for each forage category was calculated.

Snow affects bighorn sheep by increasing locomotive costs (Dailey and Hobbs 1989), and by influencing foraging efficiency (Goodson et al. 1991). We assumed snow depths on the Big Creek winter range did not impede locomotion enough to warrant inclusion in the model. However, Goodson et al. (1991) reported even light snowfall events (< 5 cm) affected nutrient intake rates of bighorn sheep in Colorado. Bighorns spent more time pawing and nosing through snow to select forage, consequently dry matter intake rates declined from 14 to 17%. Therefore, we consulted field notes and weather records to determine when foraging efficiency was reduced due to snow conditions. Where appropriate, the daily intake rate of grasses and forbs was reduced by 14%.

Model Experiments

We used planned manipulations of individual or groups of variables to examine their effect on model results, and to illustrate the processes being modeled. Similar to Hobbs (1989), we did not conduct a traditional sensitivity analysis, because different variables offered different ranges of variation, and some processes represented in the model were linear while other processes were nonlinear. In such situations, Hobbs (1989) felt that changing model parameters by equal amounts and comparing the effect of those changes on model output may provide misleading comparisons.

To illustrate the role seasonal changes in basal metabolism played in enabling bighorn ewes to maintain a positive energy balance, summer basal metabolism values were used while other model values reflected winter conditions. To examine the relationship between activity and energy, daily energy balance was graphed with time spent active each day. The effects of varying bite rates and sizes, and the effects of snow on foraging efficiency were examined by manipulating individual variables. A scenario depicting a severe winter with deep and frequent snowfall was modeled to illustrate the energetic consequences of simultaneously changing several variables. In this scenario, diet composition of curl-leaf mountain mahogany was reduced, and diet composition of bluebunch wheatgrass and Idaho fescue were increased to simulate interspecific competition for browse from elk. Concomitantly, percent of active time spent pawing through snow was increased, the energetic cost of pawing was increased, and percent of time spent feeding (i. e. actually biting vegetation) was decreased. In addition, we assumed bighorns would be confined to smaller feeding sites where snow depth was shallowest, and increased intraspecific competition for forage would result. Consequently, bite sizes, bite rates, and digestible energy values of grass species were reduced.

RESULTS

Bighorn ewes required more energy during summer, Period 1, than at any other time of year (Figure 4.1,Table 4.3). Ewes expended an average 196.75 kcal/kg$^{0.75}$/day or 4,863 kcal/day. Higher basal metabolism, lactation, and movement costs contributed substantially to energy expenditures. However, daily energy intake, 224.71 kcal/kg$^{0.75}$/day or 5554 kcal/day, generally exceeded energy expended during this time of year. Grasses and forbs contributed approximately equal amounts to daily energy intake (Table 4.4).

During late-summer-fall, Period 2, ewes used an average of 117.96 kcal/kg$^{0.75}$/day or 2,915 kcal/day. The energetic demands of lactation and basal metabolism declined, however, digestible energy of most forages also declined (Chapter 2). Nevertheless, ewes were able to meet their energy requirements with an average intake of 176.54 kcal/kg$^{0.75}$/day or 4,364 kcal/day (Figure 4.2, Table 4.3). Mean daily energy supplied by forbs was slightly higher than grasses (Table 4.4).

Bighorn ewes during winter, Period 3, sometimes did not meet their daily energy requirements (Figure 4.3), and energy balances were often only slightly positive. However, model results (Table 4.3) indicated that ewes did meet their energy needs on the majority of days by reducing their activity (Chapter 3) in conjunction with a low metabolic rate. On average, ewes expended 96.10 kcal/kg$^{0.75}$/day or 2,375 kcal/day, and obtained 113.00 kcal/kg$^{0.75}$/day or 2,793 kcal from forage. The majority of energy was obtained from grasses and secondarily from browse. Forbs contributed only 15% to energy intake during mid-winter.

During late-winter, Period 4, snowfall events continued and many perennial bunch grasses continued to offer mid-winter nutrient levels (Chapter 2). However, on southwest facing slopes some grasses, such as blue grasses, began to green-up. Nevertheless, ewes sometimes did not meet their daily energy needs (Figure 4.4). Over the entire period, ewes expended an average of 121.07 kcal/kg$^{0.75}$/day or 2,993 kcal/day, and obtained 139.56 kcal/kg$^{0.75}$/day or 3,450 kcal/day from forage (Table 4.3). Browse played an important role in meeting the energy needs of ewes during this time period, averaging 51.20 kcal/kg$^{0.75}$/day or 1,265 kcal/day (Table 4.4), which was 37% of total energy intake.

Forages were very digestible during spring green-up, Period 5, and nutrient levels were at their highest levels of the year (Chapter 2). Consequently, ewes easily exceeded daily energy needs, though they were faced with the energetic demands of the third trimester of gestation (Figure 4.5). Ewes expended 159.09 kcal/kg$^{0.75}$/day or 3,932 kcal/day and obtained 350.76 kcal/kg$^{0.75}$/day or 8,670 kcal/day (Table 4.3). Grasses furnished the vast majority of energy intake (66%; Table 4.4).

Bighorn ewes in Big Creek incurred negative daily energy balances when basal metabolism values, as represented by RMR, remained at summer levels (Figure 4.6). Ewes needed to maintain some activity in order to meet "fixed" energy costs. If ewes failed to acquire a minimum level of daily energy intake, then they risked running an energy deficit (Figure 4.7). Small changes in bite rates, bite sizes, and digestible energy estimates produced surprisingly large changes in energy intake, especially if the forage species composed a relatively large portion of the diet. For example, changing the bite size of bluebunch wheatgrass from 1.45 g to 0.69 g markedly reduced the energy consumed (Figure 4.8). During periods, such as winter and late-winter, when ewes were more likely to suffer daily energy deficits, small changes in bite rates, bite sizes, and intake rates could cause negative energy balances. Likewise, models were also sensitive to the effects of snow on intake rates. Including snow effects in the model markedly reduced energy intake (Figure 4.9), thus greatly increasing the likelihood of energy deficits. Changing the value of several variables simultaneously to reflect conditions typical of a severe winter produced uniformly negative energy balances during late winter (Figure 4.10).

DISCUSSION

The models underscore how bighorns have adapted to seasonal changes in forage quality and environmental conditions. Including seasonal changes in basal metabolism in the models (Chappel and Hudson 1978a, 1978b) played a key role in allowing ewes to meet energetic demands on the majority of days. During winter, forage quality and foraging time declined, and large energy deficits would have occurred if basal metabolism had remained at summer levels. The lower basal metabolism allowed ewes to reduce activity levels during winter, thus conserving energy. Energy demanding processes, such as lactation and gestation, occurred when forage was of high quality (Chapter 2) enabling ewes to acquire energy relatively easily. If the occurrence of these processes were timed differently, then ewes would have incurred large energy deficits.

Northern ungulates generally experience a relatively short period of abundant high quality forage in which to recover from the stresses of winter. The energy demanding processes of growth, late gestation, and lactation occur during this period, plus animals must not only recover from the previous winter, but must store energy reserves for the next. Northern ungulates may need a higher metabolism during the spring and summer in order to accomplish the necessary tissue growth before winter's onset (Renecker and Samuel 1991). Indeed, Renecker and Hudson (1986) reasoned metabolic rates for moose were not really low in winter, but that summer rates were high during the brief pulse of northern plant production.

The seasonal metabolic cycles of northern ruminants have often been accompanied by over winter weight loss (Wood et al. 1962, Hudson et al. 1985, Renecker and Samuel 1991).

This phenomenon has been reported so frequently that King and Murphy (1985) argued that biologists automatically assume endotherms face a relentless nutritional challenge to meet energy needs, and that the annual cycle necessarily includes periods of great nutritional stress. They considered typical winter weight loss an adaptation to prevent nutritional stress rather than a negative result of winter conditions.

Nevertheless, inadequate energy intake has appeared to negatively affect body condition resulting in physiological changes within an animal. Female weight and adipose fat deposition profoundly influenced fecundity and the timing of parturition. Conception and ovulation rates were closely associated with levels of fat reserves and body mass in Peary caribou (*Rangifer tarandus pearyi*; Thomas 1982), red deer (*Cervus elaphus*; Hamilton and Blaxter 1980), wapiti (Hudson 1981), and Peppin Merino sheep (*Ovis aries*; Edey 1968). Reproduction virtually ceased following hard winters when female Peary caribou were in poor condition. Cameron et al. (1993) reported the probability of a successful pregnancy for barren-ground caribou (*R. tarandus granti*) was predetermined by autumn condition. Females in good condition were more likely to ovulate and conceive.

Parturition rates appear to be quite sensitive to changes in body mass (Cameron and Ver Hoef 1994, White 1983). Female caribou and reindeer that repeatedly fail to regain energy reserves depleted by the costs of reproduction eventually undergo a breeding pause (Dauphine 1976, Reimers 1983, Cameron 1994). Given constant conditions of winter severity and forage quality, breeding pauses within a herd may be asynchronous (Cameron and Ver Hoef 1994). However, severe winters could cause cycles in parturition rates if the majority of bighorn ewes were unable to successfully reproduce in a given year, but later as a group regained sufficient energy reserves to produce lambs in a subsequent spring.

Likewise, calving date and early calf survival appeared to be determined by female condition during late gestation. Adequate nutrition during the later stages of gestation was a prerequisite for successful reproduction in elk (Thorne et al. 1976). Similarly white-tailed deer and mule deer that failed to acquire adequate energy during the last third of gestation produced fawns that survived poorly (Julander et al. 1961, Verme 1962, Holl et al. 1979). In addition, females in poor condition may fail to provide adequate maternal care following parturition (Langenau and Lerg 1976). Evolutionary pressure may force females to achieve a minimum weight or set-point before successfully reproducing and surviving (Price and White 1985, Renecker and Samuel 1991).

Few data exist on seasonal weight changes in free-ranging Rocky Mountain bighorn sheep. After parturition, 3 and 4 year-old ewes in northern Alberta lost an average of 14 kg over winter, or approximately 23% of their pre-winter body weight (Jorgenson and Wishart 1984). Approximately 6 kg of lost weight was conceptus, therefore approximately 10 to 11% of the loss was fat and muscle. Also in Alberta, Stelfox (1970) reported over winter weight losses in bighorn sheep of 20%, 11%, and 13% for Jasper, Banff, and Waterton National Parks, respectively. Bighorns in Jasper had much higher parasite loads and existed on poor range at high densities. Jorgenson and Wishart (1984) reported that older ewes lost more weight over winter than younger animals, however, older animals regained lost weight faster than younger animals in summer. This observation supports Renecker and Samuel's (1991) observation that winter weight change was negatively correlated with peak autumn weight in mule deer. Animals experiencing greater weight loss over winter demonstrated greater compensatory weight gains in spring. The energetic demands of gestation and lactation were also evident in differences between parous ewes, barren ewes, and ewes that lost their lambs early (Jorgenson and Wishart 1984). Parous ewes did not gain weight as rapidly as non-reproducing ewes.

Model results indicated that over the winter Big Creek ewes met their energy needs on most days, and therefore, probably did not suffer an extended period of winter weight loss. These results were surprising and differed from those expected for a northern ruminant. Miquelle (1990 p. 131) stated, "Accuracy of any factorial energy budget is difficult to assess. Therefore, our interest lay not in the exact values predicted by the model, but in the relative values…, and in the importance of input variables in affecting the outcome". Similarly, the models developed in this study provided insights into the bioenergetics of bighorn ewes in central Idaho by illuminating combinations of factors and influences that may cause bighorns to suffer an energy deficit.

Bighorn ewes sustained energy deficits on days when they failed to reach a minimum level of activity. Ewes needed to expend a certain amount of energy acquiring food to meet the "fixed" energetic costs that continued during inactivity. Naturally, "fixed" energy costs were higher during certain periods. During summer, energetic costs of lactation were high, occurred whether or not ewes were active, and forced ewes to acquire energy by foraging frequently. Since the majority of active time was spent foraging (Chapter 3), less activity translated into less energy obtained. A necessary condition was that ewes obtained more energy than the added energetic cost of feeding. If poor forage quality prevented meeting this condition, then logically ewes should have conserved energy reserves by remaining inactive. Ewes in Big Creek avoided this situation by displaying an adaptable plasticity in diet selection (Chapter 2). Model results emphasized the importance of forbs and browse in the diet at critical times of the year. When graminoids were of high quality during spring, ewes derived most of their energy from grasses, but as grasses cured-out over the summer, forbs supplied an increasingly important portion of energy intake. Indeed, during late summer-fall forbs furnished the majority of energy intake, even though graminoids constituted a greater percent diet composition (Chapter 2). Energy supplied by forbs enabled ewes to exist at a positive energy balance during late summer-fall, and enter the winter in better condition. Additionally, in late winter when forbs were largely unavailable, and grasses were low in digestible energy or buried under sheet ice, browse species supplied important sources of energy. Energy supplied by browse species enabled ewes to obtain adequate energy during the second and third trimesters of gestation. Therefore, browse may play an important role in fetal development, especially during severe winters.

Model results indicate that snow conditions may profoundly influence the bioenergetics of bighorn ewes. Bighorns generally avoid areas of deep snow cover, and important winter ranges are located on southwest facing slopes at low elevations or on exposed wind-blown ridges (Geist 1971). Bighorns generally continue to feed by pawing through snow, but even light snow may decrease foraging efficiency (Goodson et al. 1991). Snow may become deep enough to prevent ewes from obtaining a net energy gain while feeding. Following deep snowfall events bighorns remained inactive for extended periods of time in British Columbia (Eccles 1978). Snowfall also influences diet selection, thus affecting energy intake. Persistent snow cover caused bighorns in Colorado to shift from feeding in open areas, where green-up was advanced, to feeding in areas of shrub and tree cover (Goodson et al. 1991). By shifting habitats, bighorns increased bite sizes and intake rates, but consumed less green material. Bighorns in British Columbia increased intake of coarse bluebunch wheatgrass and shrubs following snowfall events (Eccles 1978, Wikeem and Pitt 1992). Apparently, they protruded above the snow and were more obvious to bighorns. Similar feeding behavior was observed among the Big Creek bighorns during winter (Chapter 2).

Snow depth, although important, is not the only snow characteristic that influences the bioenergetics of northern ruminants (Peek 1986). Density and hardness also play an important role in winter ecology. Thomas (1982) cited 3 conditions that reduced forage availability for Peary caribou: (1) frozen rain or wet snow in early winter that coats forage with ice, (2) deep compacted snow, and (3) sheet ice formed by freezing and thawing cycles. Following mid-winter rains, sheet-ice formed over portions of the Big Creek winter range preventing ewes from foraging in areas where they had previously fed (Wagner unpublished data).

Other authors, who constructed energy budget models, also reported that snow conditions played a key role in determining whether winter energy balances were positive or negative. Stephenson (1995) constructed a factorial energy budget model for moose on the Copper River Delta in Alaska that demonstrated moose were in positive energy balance during late winter, because actual snow depths were minimal. However, by increasing modeled snow depths to 100 cm, moose were placed in a substantial negative energy balance. In Denali National Park, where winter snow depths were consistently high, factorial energy budget models showed that moose typically ran negative energy balances each winter (Miquelle 1990, Miquelle et al. 1992).

Snow cover may cause a negative energy balance by affecting the energy intake side of the equation. Models have shown that energy balances were more sensitive to factors that determine intake rates compared to those that influence energy requirements (Fancy 1986, Hobbs 1989, Stephenson 1995, Parker 1999). Hobbs (1989) simulated the energy balance and winter survival of female mule deer and fawns in Colorado. Energetic costs of thermoregulation were relatively minor (4% of total energy expenditure for does, and 2% for fawns); and locomotion through snow contributed little to energy costs, because deer moved slowly while feeding. Nevertheless, increased snow depths resulted in increased mortality, because of snow's effect on energy intake rather than expenditure. Greater snow levels greatly impeded foraging efficiency and reduced forage availability. The intake of digestible energy was the primary nutritional factor limiting Sitka black-tailed deer (O. h. sitkensis) populations in Alaska (Parker et. al 1999). The negative energy balance was a direct result of the decrease in available high quality food when snow cover was less than carpus height (25-30 cm). However, as snow levels accumulated above 25 cm locomotion costs became significant.

During winter and late-winter, energy balances were often only slightly positive. If severe snow conditions, such as widespread sheet ice, had occurred more frequently in conjunction with poor forage quality and/or increased intra- and interspecific competition for nutrients, then a greater number of negative daily energy balances could have produced a net negative energy balance for the winter. One or several severe winters in succession could potentially deplete ewe energy reserves below a critical set-point needed to successfully conceive and nurture offspring (Price and White 1985, Renecker and Samuel 1991).

Throughout their range, many bighorn populations have experienced disease-related die-offs, and the Big Creek herd is no exception (Akenson and Akenson 1992). In some areas bighorns appeared to be in good condition and the epizootic apparently operated in a density-independent manner, because a large proportion of the population was susceptible to novel strains of the pathogen (Miller et al. 1991). In other situations, high population density preceded die-offs (Schwantje 1986), and density-dependent processes may have operated. Whether or not poor nutrition is the ultimate cause of bighorn sheep die-offs has been debated (Dunbar 1992). However, generally with non-exotic diseases a link between nutrition and disease susceptibility has been demonstrated in other mammals (Chandra and Newberne 1977).

Most likely, the effects of many epidemiological and nutritional factors interact in a complex "web" to ultimately determine bighorn sheep population fluctuations (Wobeser 1994). Assuming the models presented here are accurate, disease problems within the Big Creek bighorn herd do not appear caused by a lack of energy intake. However, bighorn densities during this study were low compared to the late 1980's (Oldenburg 1993), and energy intake values may be different at higher population densities. Preferred feeding areas may become overgrazed forcing bighorns to forage in less than optimum habitat.

MANAGEMENT IMPLICATIONS

Managers should recognize bighorns utilize forbs and browse under certain seasonal conditions in order to meet energy requirements. Habitat management should focus on providing a diverse plant community to allow bighorns flexibility in diet selection. Exotic plant invasions that reduce plant diversity (Whitson et al. 1996) should be considered a serious threat to bighorn sheep by land management agencies. Bighorn sheep ranges lying within designated wilderness areas are vulnerable to exotic invasions in spite of their relative remoteness. Wilderness legislation and/or its interpretation should be modified to enable an immediate and aggressive response to exotic plant invasions.

Winter severity for bighorn ewes in central Idaho, is largely determined by snow conditions rather than extremes of temperature. The effect of snow on bighorn sheep bioenergetics is complex and consists of multiple interacting factors. Additional research to further understand how snow affects bighorn sheep nutrition is needed. Severe winters may produce cycles in parturition rates. An observed drop in parturition rates may be blamed on predation or disease, when ultimately caused by previous severe winters. Factors that make a winter severe need to be identified and modeled.

Modeling illuminates gaps in our knowledge and organizes how we think about biological processes. The above models highlighted specific areas of needed research on bighorn sheep bioenergetics. Most basal metabolism values were published by Chappel and Hudson (1980, 1978a, 1978b, 1979, 1978c) using open circuit calorimetry, and sample sizes were small. Additional measurements of basal metabolism with the latest equipment would increase the accuracy and reliability of estimates. Furthermore, calorimetric measurements have not been made specifically for bighorn sheep for: head-down postures ("sleeping"), ruminating, pawing or cratering, and social behaviors (fighting and playing). Cost of thermoregulation during hot weather has been little researched in northern ungulates, although energetic costs of maintaining homeostasis may be considerable. Calorimetric measurements of bighorn sheep while panting would increase the accuracy of bioenergetic models. In this study, energetic costs of lactation for bighorn sheep relied upon research conducted upon mule deer (Sadlier 1980, 1982). Content and quantity of milk varies considerably among mammals (Robbins 1993). Milk production values and measurements of the energy content of bighorn sheep milk throughout the lactation cycle would increase our understanding of bighorn sheep energy requirements. Also, bighorn sheep growth rates have rarely been obtained under free-ranging conditions.

In this and previous ungulate energy models, factors that affected energy intake exerted more impact on energy balance, than processes that influenced energy requirements (Fancy 1986, Hobbs 1989, Stephenson 1995, Parker 1999). Therefore, additional research should increase the sample sizes upon which estimates of species specific bite sizes, bite rates, digestible energy estimates, and nutrient content assessments are based.

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Table 4.1 Estimated lamb size[a], mean daily milk intake[b], and equivalent daily energy intake[c] of bighorn lambs in Big Creek, Idaho from 1994-1997.

Days past birth	Lamb weight kg	Mean daily milk intake g/day	Mean daily energy intake kcal/day	Mean daily energy intake kcal/kg$^{0.75}$/day
8	5.95	775.05	1147	46.41
15	7.17	754.36	1116	45.15
25	8.89	726.05	1075	43.49
35	10.63	721.14	1067	43.17
45	12.36	538.77	797	32.25
55	14.09	435.66	645	26.10
65	15.82	360.22	533	21.56
75	17.55	301.68	447	18.09
85	19.28	236.95	351	14.20

[a] Calculated according to Blood et al. (1970).

[b] Calculated from Sadlier (1980).

[c] Calculated using 1.48 kcal/g for Dall's sheep milk from Robbins (1993).

Table 4.2 Definition of variables used to model bioenergetics of bighorn ewes in Big Creek, Idaho, 1994-1997.

Name	Definition	Units	Reference
Energy Requirements Model			
ACTIVE	Minutes active/24 hr	min	Chapter 3
AVE_DISTANCE	Average distance moved/ 24hr	km	Chapter 3
BEDD	Minutes bedded/24 hr	min	Chapter 3
COST_FEED	Energetic cost of feeding	$kcal/kg^{0.75}/min$	Chappel and Hudson (1978b)
COST_LYING	Energetic cost of lying	$kcal/kg^{0.75}/min$	Chappel and Hudson (1979)
COST_PAW	Energetic cost of pawing	$kcal/kg^{0.75}/min$	Fancy and White (1985)
COST_RUMIN	Energetic cost of rumination	$kcal/kg^{0.75}/min$	Pauls (1981), Renecker (1983)
COST _SLEEP	Energetic cost of sleeping	$kcal/kg^{0.75}/min$	Pauls (1981), Renecker (1983)
COST_SOCIAL	Energetic cost of socializing	$kcal/kg^{0.75}/min$	Estimated
COST_STAND	Energetic cost of standing	$kcal/kg^{0.75}/min$	Chappel and Hudson (1979)
DAY	Days past conception	$kcal/kg^{0.75}/min$	Calculated
DISTANCE_DOWN	Distance moved downhill/24 hr	km	Calculated
DISTANCE_HORIZ	Distance moved side-hill/24 hr	km	Calculated
DISTANCE_UP	Distance moved up-hill/24 hr	km	Calculated
DAILY_E_REQUIRED	Total daily energy required	$kcal/kg^{0.75}/min$	Output
DAILY_FEED_COST	Daily cost of feeding	$kcal/kg^{0.75}/min$	Output
DAILY_GEST_COST	Daily cost of gestation	$kcal/kg^{0.75}/min$	Output
DAILY_LYING_COST	Daily cost of lying	$kcal/kg^{0.75}/min$	Output
DAILY_PAW_COST	Daily cost of pawing	$kcal/kg^{0.75}/min$	Output
DAILY_PELAGE_COST	Daily cost of molting	$kcal/kg^{0.75}/min$	Calculated
DAILY_RUMIN_COST	Daily cost of rumination	$kcal/kg^{0.75}/min$	Output
DAILY_SLEEP_COST	Daily cost of sleeping	$kcal/kg^{0.75}/min$	Output

Table 4.2 Continued

DAILY_SOCIAL_COST	Daily cost of socializing	kcal/kg$^{0.75}$/min	Output
DAILY_STAND_COST	Daily cost of standing	kcal/kg$^{0.75}$/min	Output
DAILY_THERMO_COST	Daily cost of thermoregulation	kcal/kg$^{0.75}$/min	Output
DAY_PAST_BIRTH	Days past parturition	days	Input
HOURS_OVER_23C	Hours averaging > 23 C/day	hours	Input
LACTATION_COST	Energetic cost of lactation	kcal/kg$^{0.75}$/day	Calculated
MINS_OVER_23C	Minutes > 23/C each day	minutes	Calculated
MOVE_DOWN_COST	Down-hill movement cost	kcal/kg$^{0.75}$/day	Dailey and Hobbs (1989)
MOVE_HORIZ_COST	Side-hill movement cost	kcal/kg$^{0.75}$/day	Parker et al. (1984)
MOVE_UP_COST	Up-hill movement cost	kcal/kg$^{0.75}$/day	Dailey and Hobbs (1989)
PERCENT_BITE	% active time biting vegetation	%	Chapter 3
PERCENT_CHEW	% active time head-up chewing	%	Chapter 3
PERCENT_DOWN	% movement down-hill	%	Chapter 3
PERCENT_HORIZ	% movement side-hill	%	Chapter 3
PERCENT_PAW	% active time pawing	%	Chapter 3
PERCENT_SOCIAL	% active time socializing	%	Chapter 3
PERCENT_STAND	% active time standing	%	Chapter 3
PERCENT_TOTAL_MOVE	% active time spent moving	%	Chapter 3
PERCENT_UP	% movement up-hill	%	Chapter 3
PROPOR_RUMIN	% bedded time spent ruminating	%	Chapter 3
SLEEP	Min sleeping/24 hr	min	Input
STAND_INCREM	Standing cost added to moving	kcal/kg$^{0.75}$/min	Calculated
TOTAL_MOVE_COST	Sum of movement costs	kcal/kg$^{0.75}$/day	Output
TOTAL_TIME_MOVE	Min/24 hr spent moving	min	Calculated

Table 4.2 Continued

Energy Intake Model

ACTIVE	Min active/24 hr	min	Input
BITE_RATE$_i$	Bite rate for species i	bites/min	Input
BITE_SIZE$_i$	Bite size for species I	g/bite	Input
BROWSE_ME_INTAKE	Browse metabolizable energy	kcal	Output
DAILY_BROWSE_EINTAKE	Energy intake from shrubs	kcal	Output
DAILY_E_INTAKE	Total energy intake/24 hr	kcal	Output
DAILY_FORB_EINTAKE	Energy intake from forbs	kcal	Output
DAILY_GRASS_EINTAKE	Energy intake from grasses	kcal	Output
DIET_COMP$_i$	% of diet composed of species i	%	Chapter 2
DIGESTIBILITY$_i$	% digestible dry matter species i	%	Chapter 2
FORB_ME_INTAKE	Forb metabolizable energy	kcal	Output
GE$_i$	Gross energy species i	kcal/g	Robbins (1993)
GRASS_ME_INTAKE	Grass metabolizable energy	kcal	Output
INTAKE$_I$	Intake of species i	kcal	Output
ME$_i$	% metabolizable energy species i	%	Robbins (1993)
PERCENT_BITE	% active time biting vegetation	%	Input
TIME_FEED	Min spent biting vegetation	min	Calculated

Table 4.3 Average daily energy expended, average daily energy intake, standard error, and 95% confidence intervals (kcal/kg$^{0.75}$/day) of bighorn ewes in Big Creek, Idaho from 1994-1997.

Period[a]	Energy expended	SE	95% CI	Energy intake	SE	95% CI
1	196.75	2.12	192.34-201.16	224.71	12.97	197.74-251.68
2	117.96	2.26	113.41-122.50	176.54	6.77	162.93-190.15
3	96.10	0.31	95.48-96.71	113.00	2.40	108.23-117.76
4	121.07	0.68	119.72-122.41	139.56	3.24	133.00-146.01
5	159.09	1.36	156.33-161.86	350.76	11.92	326.49-375.03

[a] Period 1 = Summer (1 June to 15 Aug.), Period 2 = Late summer-fall (16 Aug. to 15 Nov.), Period 3 = Winter (16 Nov. to 15 Feb.), Period 4 = Late winter (16 Feb. to 31 March), period 5 = Spring green-up (1 April to 31 May).

Table 4.4 Average daily energy intake (kcal/kg$^{0.75}$/day), standard error, and 95% confidence intervals supplied by grasses, forbs, and browse of bighorn ewes in Big Creek, Idaho 1994-1997.

Period[a]	Grasses	SE	95% CI	Forbs	SE	95% CI	Browse	SE	95% CI
1	90.88	5.25	79.97-101.79	90.78	5.24	79.89-101.68	43.04	2.48	37.87-48.21
2	71.66	2.75	66.14-77.18	78.15	3.00	72.12-84.17	26.74	1.03	24.67-28.80
3	68.35	1.45	65.48-71.22	17.38	0.37	16.65-18.11	27.27	0.59	26.10-28.45
4	59.84	1.38	56.64-62.13	28.96	0.69	27.59-30.32	51.20	1.24	48.74-53.66
5	232.85	7.91	216.74-248.97	92.05	3.13	85.68-98.72	25.86	0.88	24.07-27.65

[a] Period 1 = Summer (1 June to 15 Aug.), Period 2 = Late summer-fall (16 Aug. to 15 Nov.), Period 3 = Winter (16 Nov. to 15 Feb.), Period 4 = Late winter (16 Feb. to 31 March), period 5 = Spring green-up (1 April to 31 May).

Figure 4.1 Summer (June 1 - Aug. 15) daily energy expended and energy intake of bighorn ewes from Big Creek, Idaho 1994-97

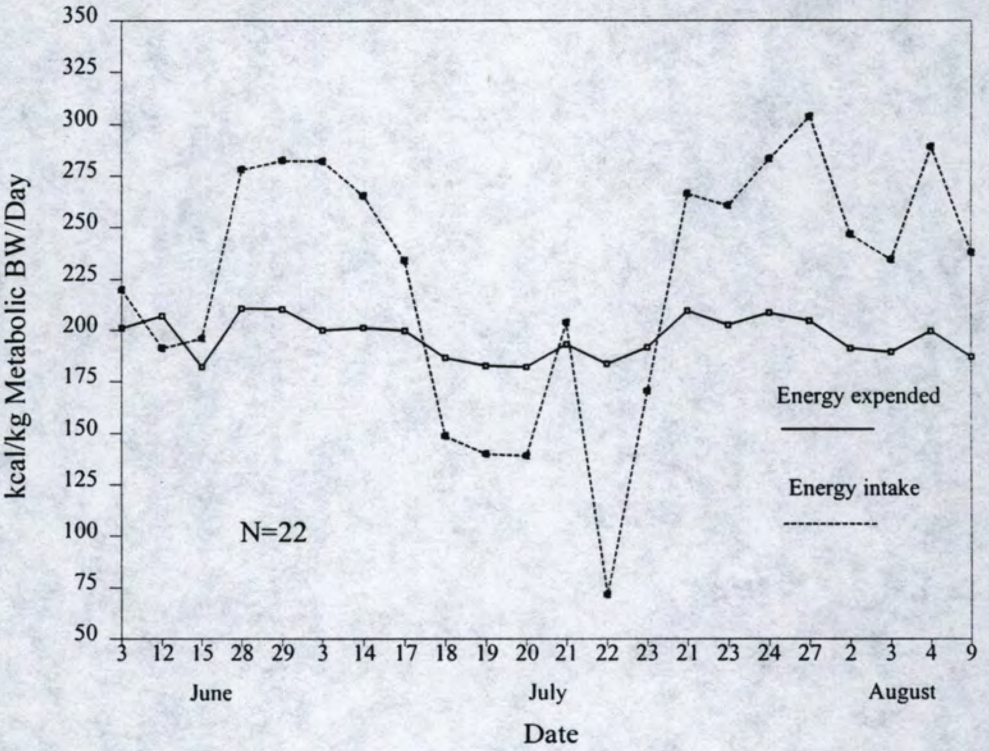


Figure 4.2 Late summer-fall (Aug. 16 - Nov. 15) daily energy expended and energy intake of bighorn ewes from Big Creek, Idaho 1994-97

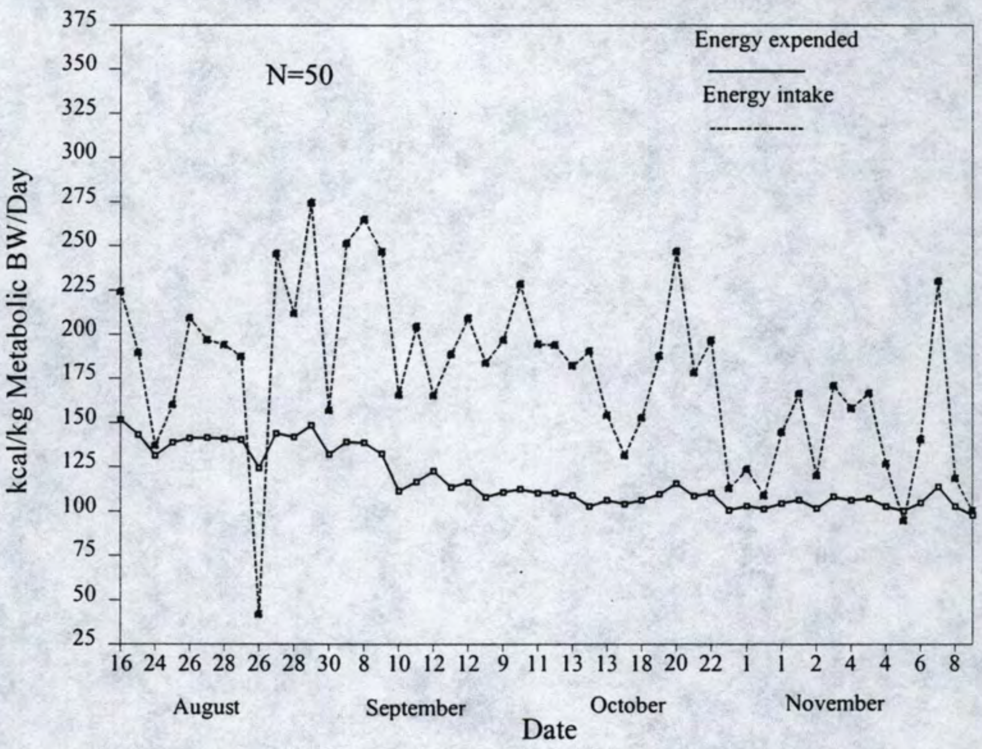


Figure 4.3 Winter (Nov. 16 - Feb. 15) daily energy expended and energy intake of bighorn ewes from Big Creek, Idaho 1994-97

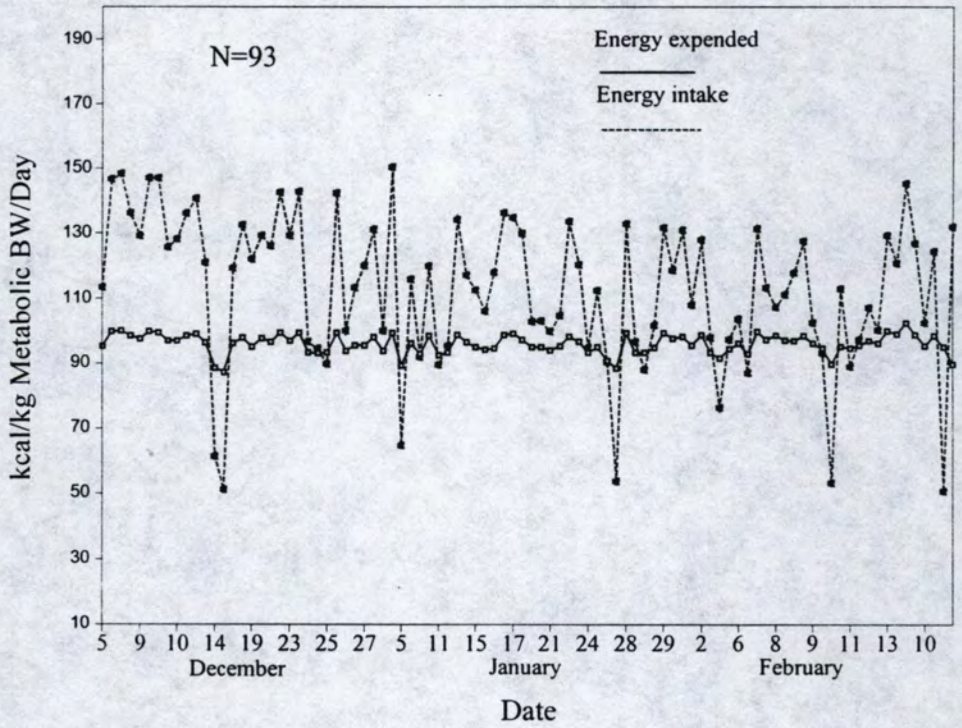


Figure 4.4 Late winter (Feb. 16 - March 31) Daily energy expended and energy intake of bighorn ewes from Big Creek, Idaho 1994-97

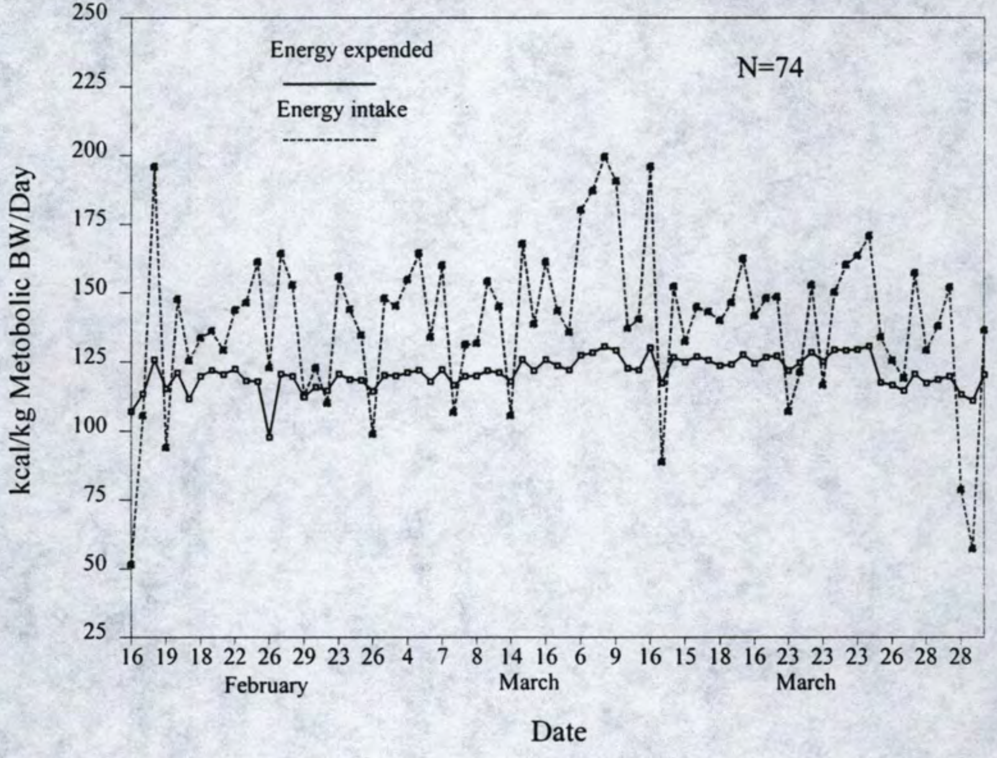


Figure 4.5 Spring green-up (April 1 - May 31) Daily energy expended and energy intake of bighorn ewes from Big Creek, Idaho 1994-97

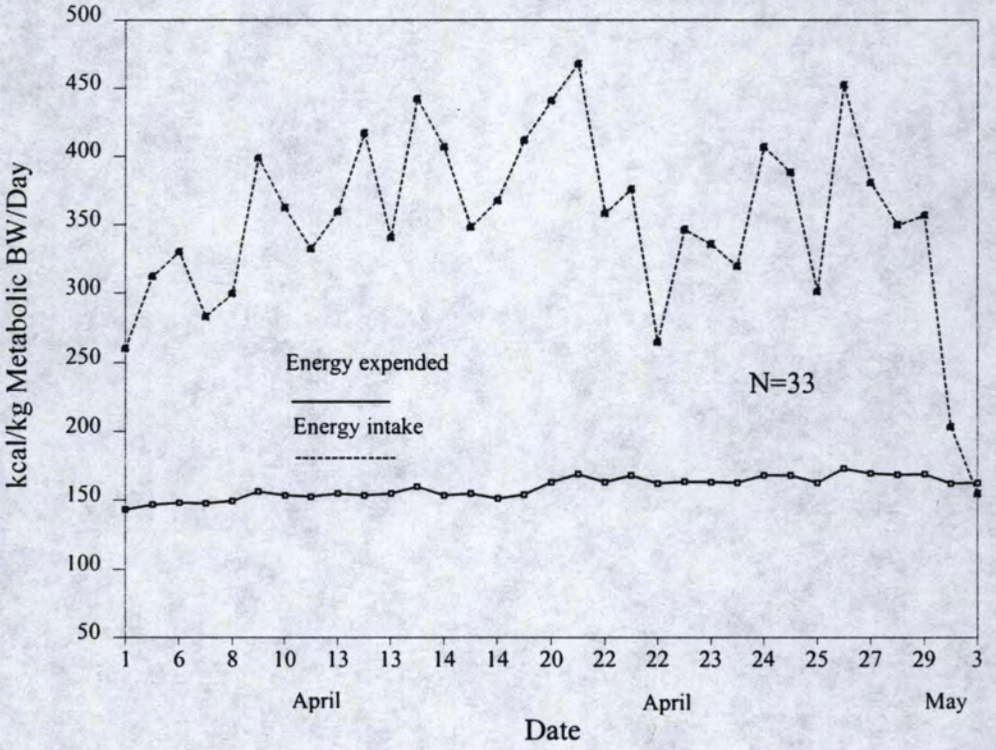


Figure 4.6 Winter (Nov. 16 - Feb. 15) energetics using summer basal metabolism values for bighorn ewes from Big Creek, Idaho 1994-97

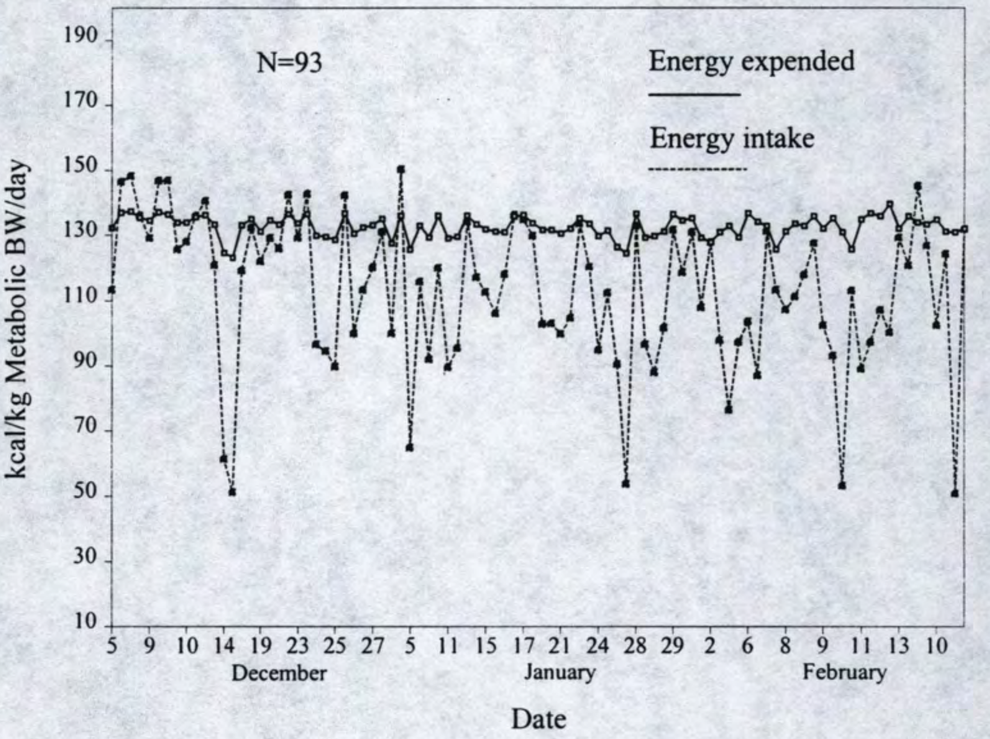
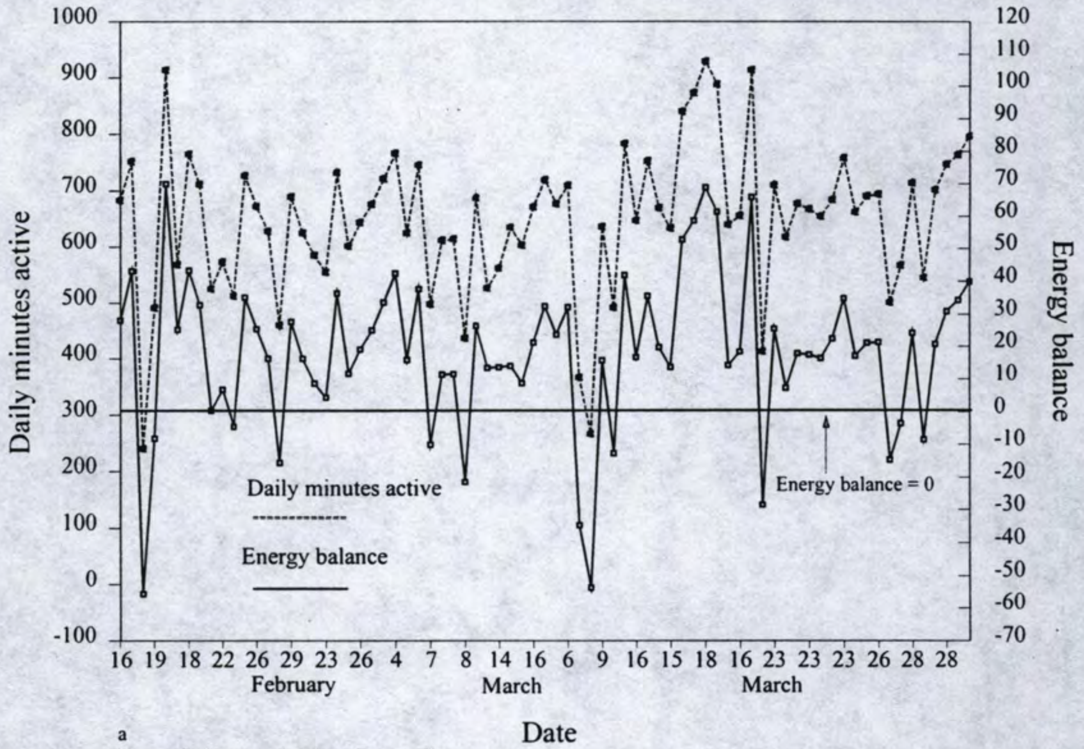


Figure 4.7 Late winter (Feb. 16 - March 31) daily minutes active and energy balance[a] of bighorn ewes from Big Creek, Idaho 1994-97



[a] Energy balance = Intake - Expenditure

Figure 4.8 Late summer-fall (Aug. 16 - Nov. 15) effect of bite size on energy intake of bighorn ewes from Big Creek, Idaho 1994-97

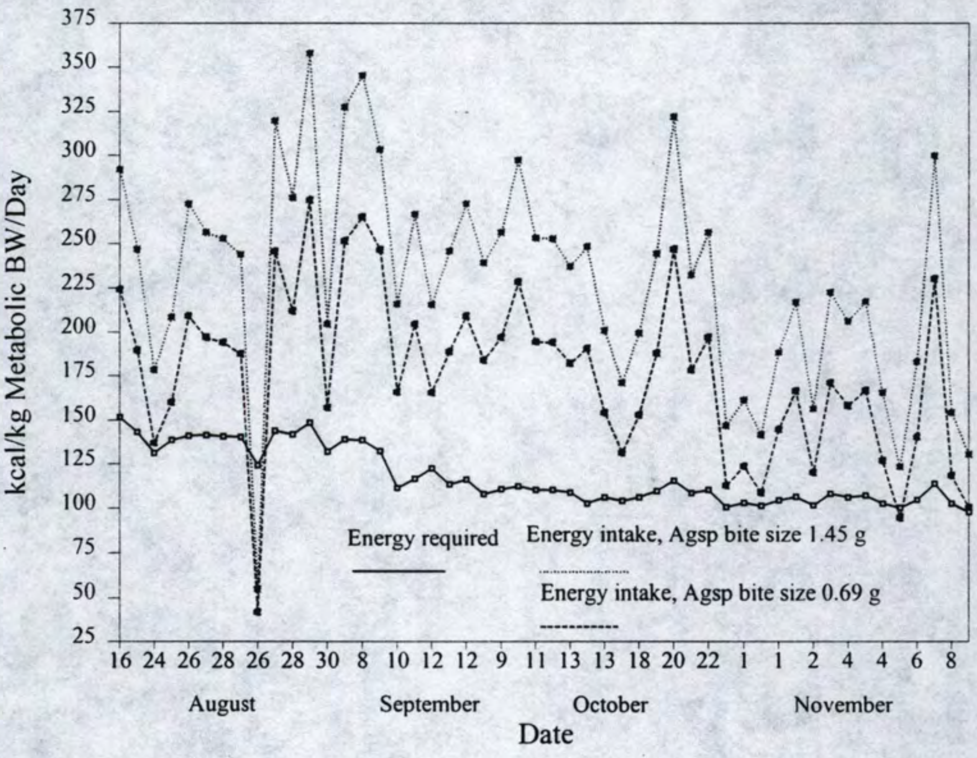


Figure 4.9 Late winter (Feb. - March 31) effects of snow on daily energy intake of bighorn ewes from Big Creek, Idaho 1994-97

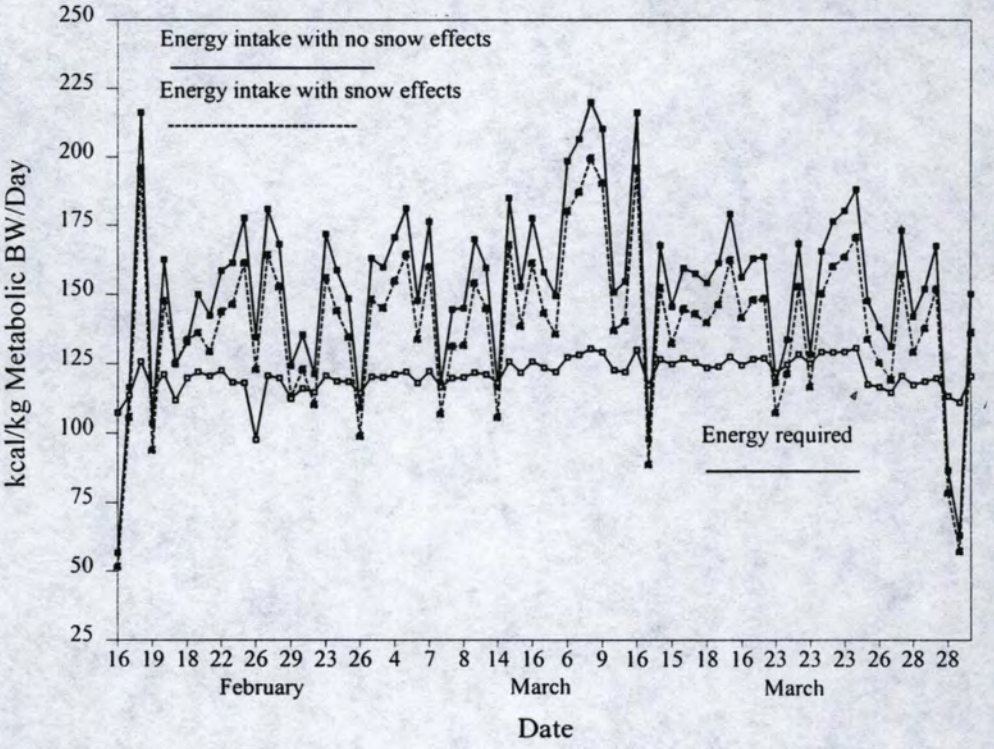
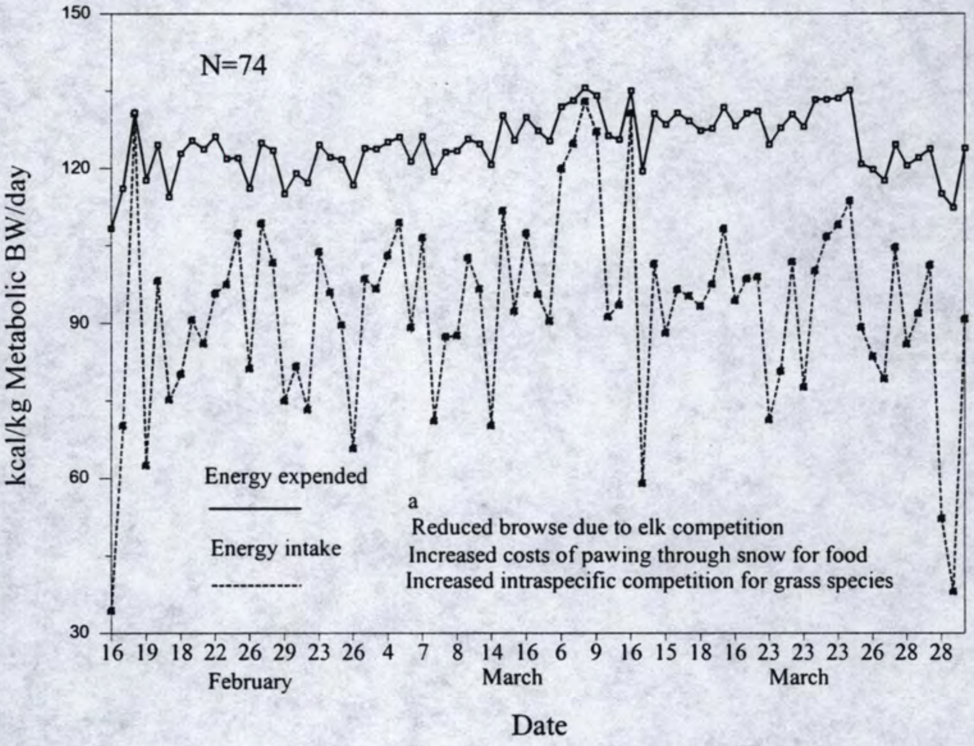


Figure 4.10 Late winter energy intake and expenditure under severe conditions for bighorn ewes from Big Creek, Idaho 1994-97[a]



a
Reduced browse due to elk competition
Increased costs of pawing through snow for food
Increased intraspecific competition for grass species