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EFFECTS OF VARIATION IN FOOD QUALITY ON GROWTH AND SURVIVAL OF COLUMBIAN GROUND SQUIRRELS

BY

Ronald P. Bennett ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science.

DEPARTMENT OF BIOLOGICAL SCIENCES

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled EFFECTS OF VARIATION IN FOOD QUALITY ON GROWTH AND SURVIVAL OF COLUMBIAN GROUND SQUIRRELS submitted by Ronald P. Bennett in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

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August 5, 1997

Abstract

Overwinter survivorship of juvenile Columbian ground squirrels (Spermophilus columbianus) is positively related to prehibernation weight, which is primarily determined by growth rate after emergence from natal burrows. This study examined how food quality influences growth and survival of juvenile Columbian ground squirrels, and reproductive success of their dams. Growth and survival of juveniles was enhanced on sites with more forbs; forbs contain 15-40% more protein and are 30-50% more digestible than grasses, and squirrels selectively foraged for forbs. Juveniles supplemented with highly digestible, energy-rich food exhibited growth and survival rates similar to juveniles on sites with high forb content. Manipulation of dietary protein of captive juveniles produced no difference in growth rates among treatments, or from the highest rates observed in the field. Results indicate that forbs are a high quality food, and that digestibility is a more important food quality indicator for juvenile ground squirrels than either energy or protein.

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Chapter 1: General Introduction

Female reproductive success is a major component of population dynamics (Clutton-Brock 1988) and one that is strongly influenced by the available food supply (Pease et al. 1973, Keith et al. 1984, Smith et al. 1988, Boutin 1990). Changes in food supply can cause the reproductive success of female Columbian ground squirrels (Spermophilus columbianus) to vary (Dobson & Kjelgaard 1985a & b). Several factors (fecundity, mating success, longevity, and offspring survival) contribute to variation in female reproductive success (Clutton-Brock 1988). King et al. (1991) quantified lifetime reproductive success of female Columbian ground squirrels using the number of yearlings a female produced over her lifetime and found that the main source of variation was the overwinter survival of juveniles.

Overwinter survival of juveniles is related to weight at hibernation (Murie & Boag 1984) which is largely a function of juvenile growth rate. Maximum growth rates of juveniles are probably established by physiological limits to cellular metabolism which are determined by the individual's genotype (Ricklefs 1968, 1973). Realized growth rates may represent a tradeoff between maximizing growth rate and maximizing lifespan (Dickerson 1954 in Case 1978, Eklund & Bradford 1977). This tradeoff may lead to development of optimal rather than maximal growth rates that balance investment in juvenile growth against investment in survivorship and future reproduction (Case 1978).

In addition to the genetic component, development and expression of optimal growth rates is also a function of nutrient availability (Robbins 1993), which in turn depends on both quantity and quality of the food supply. Although both food quantity and quality can affect growth, for juveniles in particular, quality is more often a limiting factor (White 1978). Therefore food quality is likely more important than food quantity in attaining optimal growth rates.

Food quality is defined in various ways, but three of the primary indicators are protein content, energy content, and digestibility (Robbins 1993). These dietary variables could influence female reproductive success in several ways. High protein content could be beneficial to juveniles through its importance to growth (White 1978) whereas high energy content could be important for reproduction in adults (Ritchie 1990). Digestibility may be a better indicator of food quality for juveniles than for adult squirrels because gut capacity is likely to be an important constraint for small individuals (Belovsky 1986). In this study I examine the relationship between these indicators of food quality and growth rates of juvenile Columbian ground squirrels, and how this relationship affects the reproductive success of these juveniles' dams.

I studied Columbian ground squirrels in the Sheep River Wildlife Sanctuary (32 km west of Turner Valley, Alberta) because previous research in this area (Hare 1992, Murie unpublished data) indicated marked differences between colonies in overwinter survivorship of juvenile ground squirrels. These colonies are all adjacent to the Sheep River, in close proximity to each other (<6 km apart), and at similar elevations (1500- 1570 m), so climatic variation is unlikely to explain these differences. Preliminary research (Bennett unpublished data) also indicated differences in forage composition and quality between colonies. Thus, these colonies offered a good opportunity to study food quality and female reproductive success.

In succeeding chapters, I present different aspects of my study on Columbian ground squirrels. Chapter 2 examines relationships between natural variation in food quality and growth dynamics of juveniles in ground squirrel colonies that were known to differ greatly in overwinter survival of juveniles. Effects of food supplementation on a ground squirrel population with low juvenile survival are described in Chapter 3. A laboratory study of effects on juvenile growth of varying protein content of food is the focus of Chapter 4. Chapter 5 examines the ability of female ground squirrels to assess food quality and choose high quality food. The concluding chapter explains how the specific questions addressed in previous chapters pertain to the overall relationship between food quality and reproductive success of female S. columbianus and what further research would help to clarify that relationship.

Literature Cited

Belovsky, G.E. 1986. Optimal foraging and community structures: implications for a guild of generalist grassland herbivores. Oecologia 70:35-52.

Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Can. J. Zool. 68:203-220.

Case, T.J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. Quar. Rev. Biol. 53:243-282.

Clutton-Brock, T.H. (ed.) 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago. 538pp.

Dickerson, G.E. 1954. Hereditary mechanisms in animal growth. In B.J. Boell (ed.), Dynamics of growth processes. Princeton University Press, Princeton. p. 242-276.

Dobson, F.S. and Kjelgaard, K.D. 1985a. The influence of food resources on population dynamics in Columbian ground squirrels . Can. J. Zool. 63:2095-2104.

_____. 1985b. The influence of food resources on life history in Columbian ground squirrels. Can. J. Zool. 63:2105-2109.

Eklund, J. and Bradford, G.E. 1977. Longevity and lifetime body weight in mice selected for rapid growth. Nature 265:48-49.

Hare, J.F. 1992. Social discrimination by Spermophilus columbianus. Ph.D. thesis,University of Alberta, Edmonton.

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

King, W.J., Festa-Bianchet, M. and Hatfield, S. 1991. Determinants of reproductive success in female Columbian ground squirrels. Oecologia 86:528-534.

Murie, J.O. and Boag, D.A. 1984. The relationship of body weight to overwinter survival in Columbian ground squirrels. J. Mamm. 65:688-690.

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

Ricklefs, R.E. 1968. Patterns of growth in birds. Ibis 110:419-451.

_____.1973. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 115:177-210.

Ritchie, M.E. 1990. Optimal foraging and fitness in Columbian ground squirrels. Oecologia 82:56-67.

Robbins, C.T. 1993. Wildlife feeding and nutrition. 2nd.ed. Academic Press Inc., San Diego. pp.352.

Smith, J.N.M., Krebs, C.J., Sinclair, A.R.E. and Boonstra, R. 1988. Population biology of snowshoe hares. II. Interactions with winter food plants. J. Anim. Ecol. 57:269-286.

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

Chapter 2: Effects of Variation in Natural Food Supply on Life Histories of Columbian Ground Squirrels

Introduction

Natural populations of Columbian ground squirrels vary in growth and reproduction (Boag & Murie 1981a, 1981b) and increase in response to experimentally increased food supply (Dobson & Kjelgaard 1985a, 1985b). Regional and individual variation may result from differences in the quality of food consumed by ground squirrels (Dobson 1988). Plants available to ground squirrels vary in quality (Belovsky 1986); within the range of this variation an optimal diet may exist (Ritchie 1988). Departure from this optimal diet can reduce individual growth rates, litter sizes and survivorship (Ritchie 1990).

Achieving an optimal diet usually requires selective foraging, a behavior that has been documented in Columbian ground squirrels (Lambeth & Hironaka 1982, Elliott & Flinders 1985, Harestad 1986, Andrusiak & Harestad 1989). However, ground squirrels can only select food within the range of quality available in their habitat. If food quality is lower than optimal values, life history traits such as growth and survivorship could be altered (Dobson & Kjelgaard 1985b). Examining relationships between natural variation in food supply and ground squirrel life history traits may indicate food quality parameters that are useful for evaluating optimal diets of Columbian ground squirrels.

Ritchie (1988) used the ratio of forbs (Class Dicotyledoneae) to grasses (Class Monocotyledoneae) in ground squirrel diets as a measure of their ability to select an optimal diet. This was based on estimates of digestible energy content that indicated significant differences (forbs: 20.1 kJ/g, grasses: 18.4 kJ/g) between these two plant groups (Belovsky 1986). However, protein content (Millar & Zwickel 1972, Bergeron & Jodoin 1987, Eshelman & Jenkins 1989) and digestibility (Karasov 1985, Bucyanayandi & Bergeron 1990), which may be better indicators of food quality, were not evaluated in Ritchie's (1988) study. While forb:grass ratio is a useful gross indicator of food quality, further investigation is required to understand which differences between these plant groups are most important to ground squirrel fitness.

Food supply-ground squirrel interactions can be assessed at two different levels: population and individual. At the population level, sites where squirrels have both higher growth rates and overwinter survival may have better quality food; finding those quality factors that differ the most between sites may be sufficient to assess their relative importance. However, if the importance of quality factors varies as nutritional requirements of squirrels vary, then the process of ranking food quality indicators is improved by also examining responses of squirrels based on differences in age, sex and reproductive status.

Size, type of growth (structural growth vs. fattening), and reproductive status (gestation and lactation) of ground squirrels are useful correlates for assessing food quality (Dobson 1992). Relationships between weights of ground squirrels and energy content, protein content and digestibility of plants they consume may depend on the physiological or reproductive status of squirrels (see Chapter 1). Because growth rates of juveniles influence female reproductive success (Murie & Boag 1984, King et al. 1991), determining those factors that most effect juvenile growth is particularly relevant in evaluating intersite differences.

To investigate which food quality parameters affect growth and survival of juvenile ground squirrels most, I studied relationships between natural food supply and life history traits of ground squirrels. Effects of variation in food quality were assessed by examining between and within colony differences. Two types of disturbance (grazing by domestic livestock and controlled burns) were studied because of their potential to affect forage, and consequently the life histories of ground squirrels (Johnson & Smith 1977, Lambeth & Hironaka 1982).

Methods

Study Sites

Populations of Columbian ground squirrels in the Sheep River Wildlife Sanctuary (Figure 2.1) were studied on a limited basis from early June to mid-August in 1994 and, more extensively, from mid-April to mid-August in 1995 and 1996. The Hayfield (HF) population lives on the 72 ha grassy meadow studied by Boag & Murie (1981a & b). Four separate study grids were established within HF. In 1994, data on ground squirrels were collected from one HF grid, Gorge. Two other HF grids, Road (2.0 ha) and North (1.1 ha), were used in 1995 and 1996 to gather data on ground squirrels and forage. The remaining grid, Station (1.9 ha), and Gorge (1.7 ha) were used in 1995 and 1996 to collect forage data; ground squirrels on Station and Gorge were supplemented with food in 1995 and 1996 for another part of my study

(Chapter 3). Main burrows of ground squirrels on HF grids were located using trapping records and observations and were marked with flags on metal stakes.

The other populations used in this study were Meadow B (MB) and Meadow C (MC). The MB population lives on the 0.75 ha meadow ≅3 km west of HF described by Wiggett and Boag (1986); MC is a 0.50 ha meadow ≅2 km west of MB. Ground squirrel and forage data were collected from MC and MB. Both MB and MC were marked in 10m x 10m grids with flags like those used on HF.

Ground Squirrels

Ground squirrels were live-trapped, and marked with individually numbered eartags. Ages of some squirrels were known from previous studies (Hare unpublished data, Murie unpublished data). Individuals that were untagged at first capture were assigned a minimum age based on sex and weight (Boag & Murie 1981a). Trapping was done weekly in 1995 and 1996 (trapping was less frequent in 1994) on each area. Trapping was more frequent during spring emergence and during periods when juveniles were emerging from natal burrows. Juveniles were trapped and tagged as soon after emergence as possible. When a squirrel was captured, it was weighed to the nearest 5 g using a Pesola scale, its sex was recorded, and lactation status of females was assessed based on condition of mammae (Murie & Harris 1982). Except for trapping emerging juveniles, trapping was limited to morning periods to minimize effects of amount of food in the gut on total weight.

Squirrels captured on MC and MB were considered to be residents because these sites were discrete meadows surrounded by forest. However, HF grids were smaller parts of a large continuous habitat so it was necessary to define residency. Squirrels were considered to be resident on a HF grid if they were captured at least three times within one year with at least two weeks between the first and last captures.

Overwinter survival was estimated for ground squirrels living on study sites during the summers of 1994 and 1995. Rates of overwinter survival as calculated for this study are relative indicators rather than absolute measures of overwinter loss (Appendix A.1). Survival rates of juveniles were calculated by dividing the number of yearlings that emerged from hibernation in the spring by the total number of juveniles that emerged from natal burrows the previous summer. Adult survival rates were calculated by dividing the number of adults that emerged from hibernation by the number that were resident during the previous summer. Survival rates were not calculated for yearlings because their tendency to disperse (Festa-Bianchet & King 1984) makes accurate estimation of survival difficult.

Percentage of females weaning juveniles (weaning rate) was determined by dividing the number of females that successfully raised juveniles to emergence by the number of adult (>1 year old) females living on each site at the time of juvenile emergence. Litter sizes were determined from trapping records (proximity of females to emerging juveniles and natal burrows) and observation of interactions between females and juveniles. Weaning rates and litter sizes were compared to evaluate effects of food quality differences on reproduction. Yearling females were excluded from analyses of weaning rates and litter sizes because reproduction by yearlings is rare in this geographic region (Boag & Murie unpublished data cited in Festa-Bianchet 1981). Trapping effort on HF in 1994 was insufficient to collect data on weaning rates and litter sizes.

Trapping records were used to calculate weight changes of individuals. Although the emphasis of this study was reproductive females and juveniles, some data were available on other ages and sexes of squirrels and rates of weight gain were also calculated for these squirrels. The difference between weight recorded closest (±3 days) to the beginning of a specific two-week interval and weight closest to the end (±3 days) of that interval was divided by the number of intervening days (mean = 13.52 days, range = 11-17 days) to give a daily rate of weight change (g/day). Rates were calculated for each two week period from May 1 to August 15 for yearlings and adults of each sex. Adult females were also divided into groups based on success (reproductive) or failure (non-reproductive) in weaning juveniles. Rates were compared to investigate intersite differences in weight gain that could differ depending on squirrel age or reproductive status.

Juvenile growth rates were calculated for three successive two-week intervals after emergence from natal burrows; this covered the 40 to 50 day period they are normally active before hibernation (Dobson et al. 1992). Rates were calculated in the same manner as for adults and yearlings with emergence weights (≤4 days after emergence) serving as beginning weights for the first interval. These measures of juvenile growth were used to compare growth patterns between sites. Rate of growth to maximum weight before hibernation was also determined. For juveniles recaptured ≥35 days after emergence, the difference between maximum weight and emergence weight was divided by the number of days between weighing as an estimate of growth rate to maximum weight. These rates were used to assess intersite differences in the ability of juvenile ground squirrels to maximize growth through the entire active season. If emergence weights are similar, growth to maximum weight is also likely to be a good indicator of prehibernatory weights which are important to overwinter survival (Murie & Boag 1984). Accurate direct estimates of prehibernatory weights are difficult to make because trappability decreases (pers. obs.) in the period preceding immergence. Data from both sexes of juveniles were pooled because their growth patterns do not differ (Koeppl & Hoffmann 1981). Because of the limited trapping program in 1994, only data on growth of juveniles to maximum weight is presented.

Forage

In 1995, forage samples were collected from wire mesh (2.5 cm mesh) exclosures that each covered an area of 0.1 m^2. Twenty exclosures were placed on MC, 20 on MB, and 8 on each HF site in mid-May. For MB and MC, locations of exclosures were determined by random draw of grid locations. On HF, active main burrows were randomly selected as focal points for forage sampling and samples were taken in a 5 m radius around selected burrows. At the beginning of June (15 days later), all plant material >1 cm above the ground within each exclosure was collected and the exclosure was moved to an adjacent location within a 1m radius of the original sample point. This process was repeated 5 times at 15-day intervals until mid-August when most ground squirrels had entered hibernation. If cattle displaced an exclosure before the next cutting date then the forage in that exclosure was not collected. Because of this constraint, some intervals have smaller sample sizes than those specified above.

To reduce the potential for bias in the data due to possible microclimate effects of exclosures, most forage samples were not collected from exclosures in 1996. Ten sample points per site were randomly selected on MC, MB and two HF grids. All samples were collected within a 1 m radius of randomly selected sample points at 15 day intervals from the beginning of June to mid-August. In addition to intersite comparisons, HF sample points were used to evaluate effects of a controlled burn conducted by the Alberta Forest Service on April 29, 1996 that burned varying portions (Road ≅90%, Station ≅70%) of HF grids. Twenty sample points were distributed equally in burned and unburned areas on Road and Station.

Unlike HF, MC and MB were grazed by cattle from the end of June through the remainder of the active season of squirrels during each year of the study; additional samples were taken from MC and MB in 1996 to assess effects of cattle grazing on forage quality. Sixty (thirty per site) of the exclosures used in 1995 were placed on MC and MB when cattle grazing commenced (≅ June 30). Three exclosures were placed in a 1m radius around each sampling point and forage from within one exclosure per sampling point was collected at the same time as control samples were taken. In this way, I obtained samples that were not exposed to grazing for two, four, and six weeks, respectively, for comparison to control samples collected at the same time.

All forage samples were oven-dried at 40^0 C for 48h (Allen 1989) and dead plant material was removed and weighed. The remainder was separated into grasses and forbs and weighed to estimate biomass (g/m^2). Forbs and grasses were analyzed separately because of expected differences in their nutritional characteristics (Batzli & Cole 1979, Belovsky 1986) and potential for preferential foraging by ground squirrels (Andrusiak & Harestad 1989, Ritchie 1990). For some samples, insufficient plant material was available to carry out some or all of the quality analyses. These samples were pooled with samples from the nearest adjacent points within the same grid before the analyses were done.

Samples were analyzed for crude protein content, gross energy content and digestibility. Crude protein content was assessed on a Leco Model FP-428 nitrogen analyzer which burned a small amount of forage (≅ 0.1g) in a combustion chamber, measured the amount of nitrogen released and converted this to percent plant protein (Leco Corp. 1992). Gross energy content was assessed using a bomb calorimeter that burns plant material (≅ 1.0 g) in a combustion vessel immersed in a water bath, measures temperature change (indicative of the heat released) in the water bath, and converts this to a value (kcal/g) for energy content (Allen 1989).

Digestibility was measured using the pepsin-cellulase method (Jones & Hayward 1975 as modified by Allison & Borzucki 1978). Plant material (≅ 0.2 g) was placed in a sealed 50 ml glass vial with 20 ml of a pepsin-HCl solution that was made by dissolving sufficient pepsin (Sigma Ltd. P-6887) in 0.1 M HCl to achieve 6200 enzyme activity units/ml HCl. Samples were then incubated at 40 °C for 24 h. After incubation, pH of solutions in each vial were increased by adding 1.0 M NaOH (2.0-2.5 ml) until pH of ≅5.0 was reached. Twenty ml of cellulase solution was added to each vial; cellulase (Sigma Ltd. C-0898) was dissolved in citrate-phosphate buffer (Sigma Ltd. P-4809, 1 tablet/100 ml deionized water) using amounts required to produce a solution with an enzyme activity level of 0.125 units/ml buffer. The vials were incubated for a further 48 h at 40 °C. During both incubation periods, vials were shaken lightly every 12 h. After the second incubation period, samples were vacuum filtered onto pre-weighed filter papers (Whatman #1). Samples and filter papers were dried at 40 °C for 24 h, weighed, and weights of filter papers subtracted to provide final weights for plant samples. Initial weight of the plant sample minus the final weight indicated the amount of plant material digested by enzyme solutions. This value was converted to a percent of the initial sample weight.

Results from quality analyses were combined to give other measures of food quality. Crude protein content multiplied by digestibility gave crude estimates of digestible protein (%). Digestible protein values combined with biomass values gave estimates of total digestible protein content (g/m^2). Gross energy combined with digestibility, and digestibility and biomass, gave measures of digestible energy (kcal/g) and total digestible energy content (kcal/m^2), respectively. When individual samples were too small to analyze for protein, energy or digestibility, mean values for the specific site and cutting date were used to generate estimates of total digestible protein content and total digestible energy content. For intersite comparisons (except for partial correlations) in 1996, only data from non-exclosure areas on MC and MB and burned areas on HF were used because they comprised the majority of areas where ground squirrels were monitored.

All data were tested for normality and homogeneity of variances before analysis. Based on these tests, data were compared either directly using parametric statistics (e.g. repeated measures or nested ANOVA) or after being transformed (Zar 1984). For nested or repeated measures ANOVAs with unbalanced designs or unequal sample sizes, data were compared using the GLM procedure of SPSS (1996). Comparisons of juvenile growth rates were done using individual rates nested within litters. Comparisons of forage variables were done using repeated measures ANOVAs with samples blocked by sites. Tukey's H.S.D. test was used for post-hoc comparisons after significant ANOVAs. Log-linear analyses were used to compare survival and weaning rates. All test results were evaluated at the 0.05 level of significance.

Results

Squirrels

Overwinter survival rates (Table 2.1) differed among ages and sexes. Adult male survival was significantly lower (G= 6.31, p=0.04) on MC than on other areas for the winter of 1994-95, but not for 1995-96 (G=1.36, p=0.51) although trends were similar. No differences (1994-95: G=4.24, p=0.12, 1995-96: G=1.13, p=0.57) in survival rates among areas were found for adult females. Both MC and MB juveniles had survival rates four times greater than HF juveniles in 1994-95 (G=16.91, p=0.0002) and 1995-96 (G=27.52, p<0.0001); MC and MB were similar in juvenile survivorship.

Female reproductive rates did not differ significantly between sites (Table 2.2). Weaning rates were similar for all sites in 1995 (G=1.13, p=0.57) and 1996 (G=0.59, p=0.74), and decreased on all grids in 1996. HF had lower litter sizes, but these differences were not large in either 1995 (F=2.08, p=0.14) or 1996 (F=1.91, p=0.17).

Due to small sample sizes or non-significant differences between years, data for rate of weight gain were pooled for 1995 and 1996 for all groups except reproductive adult females and juveniles. Adult males (Appendix A.2) on HF showed lower (F=12.38, p<0.001) rates of weight change than those on MC and MB, most notably in the second part of the season. Unlike older males, yearlings (Appendix A.3) showed no differences among sites (F=1.91, p=0.24) in weight change. Neither yearling (Appendix A.4: F=0.21, p=0.82) nor non-reproductive adult females (Appendix A.5: F= 0.94, p=0.41) differed in weight gain between sites. Reproductive HF females appeared to recover weight more slowly in the second half of summer, the post-lactation period, than those on MC and MB (Appendix A.6). Although the trend was similar in both years, differences were only significant in 1995 (1995: F=3.75, p=0.04, 1996: F=0.52, p=0.61). Structural size of reproductive females was compared using weight at juvenile emergence (± 4 days) because it indicates body size more accurately than late summer weights (Dobson 1992). Mean weights of MB females (498 ±9 g, n=20) were significantly (1995 & 1996 pooled, F=7.10, p=0.002) larger than weights of either MC (462 ±9 g, n=15) or HF (454 ±9 g, n=28) reproductive females.

HF squirrels, regardless of age, sex or reproductive status, appeared to have longer active seasons than those on MC and MB. Spring emergence seemed to be slightly later (7-10 days) on HF than on MC and MB, but accurate estimates of spring emergence were not possible due to adverse spring weather that limited trapping. Despite later emergence, HF squirrels probably had a longer active season due to much later immergence. Later immergence is indicated by generally larger sample sizes of HF squirrels than of MB and MC squirrels for the last weight intervals. Observations also suggest later immergence of HF squirrels because many HF squirrels were still active ≅2 weeks after the majority of MB and MC squirrels had apparently entered hibernation (pers. obs.).

Emergence weights of juveniles were similar among sites in 1994 (F=2.01, p=0.15), 1995 (F=0.12, p=0.88)and 1996 (F=0.35, p=0.71), but growth rates differed markedly (Table 2.3). Comparisons for all three years (1994: F=7.40, p=0.002, 1995: F=7.67, p=0.002, 1996: F=15.99, p<0.001) indicated that growth rates to maximum weight of MB and MC juveniles were ≅50% higher than rates for juveniles born on HF. MC and MB juveniles did not differ in growth to maximum weight, but there were some differences in the biweekly comparisons.

Both years' data for biweekly weight gain were pooled because year was a non-significant factor (F=0.15, p=0.70). Repeated measures ANOVA indicated significant differences between sites (F=15.36, p<0.001). Post-hoc comparisons revealed seasonal variation in magnitude and pattern of differences (Figure 2.2). In the first two weeks after emergence, MC juveniles grew faster than both MB and HF juveniles and MB juveniles grew faster than those on HF. During the second two week period, the difference between MC and MB growth rates was negligible, but both rates were still significantly higher than HF. In the last interval, growth rates on the 3 sites no longer differed owing mainly to reduced growth of MC and MB juveniles in 1996 and a relatively high value for the only HF juvenile assessed during this interval in 1996 (Table 2.3).

A major assumption of this study is that faster post-weaning growth produces larger prehibernatory weights in juveniles. This assumption was tested by comparing maximum weights of juveniles recaptured ≥35 days after emergence in 1995. Mean maximum weights of MC (384 ±11 g, n=16) and MB (392 ±10, n=28) juveniles were both significantly (F=9.68, p<0.001) higher than those of HF juveniles (311 ±15, n=9).

Forage

Forage on the three sites differed in many ways including seasonal variation of biomass and quality. Plant litter, the amount of dead material in the samples (Appendix B.1), was up to 10 times greater on HF than either MC or MB in 1995 (F=169.10, p<0.001). Unlike 1995, there was no significant difference between sites in 1996 (F=1.86, p=0.18). This between year difference probably resulted from using burned sites on HF for intersite comparisons. Burned areas had lower amounts of dead material than unburned areas (F=51.51, p<0.001). A reduction in dead material was also noted on areas experiencing grazing; grazed areas had ≅50% less plant litter than ungrazed areas (Appendix B.1, F=8.80, p=0.006).

Plant biomass, an estimate of total live forage available (Table 2.4), differed among sites in both 1995 (F=35.32, p<0.001) and 1996 (F=17.10, p<0.001). Post-hoc comparisons indicated variation throughout each year, but MB usually had lower plant biomass than either MC or HF. Some declines in biomass were evident on MB and MC for the last 2 and last 3 cuttings for 1995 and 1996 respectively; these declines occurred after the commencement of cattle grazing. The ungrazed site, HF, showed continual increase in biomass through most of each summer. Grazing effects on MC and MB were also evident in the 1996 grazing trial. Ungrazed sites (exclosures) had biomass values up to 5 times greater than grazed sites (F=29.80, p<0.001). Burning did not affect biomass (F=0.01, p=0.92) as burned sites recovered quickly after an initial reduction.

Composition of plant biomass was compared using percentage of forbs in the biomass as the dependent variable (Table 2.5). Distribution of forbs appeared to vary markedly on HF with many sites lacking forbs;

this was reflected in relatively high levels of variation around HF means (1995 range of C.V. values: MC=32-90%, MB=46-88%, HF=150-200%). In 1995, forb content of HF samples was 4 to 10 times lower (F=39.88, p<0.001) than samples from other sites. Post-hoc tests indicated varying levels and direction of difference between MC and MB, but both were always higher than HF.

Variation between sites lessened in 1996 with HF having higher levels of forbs, but sites still differed (F=8.58, p=0.001). Based on Tukey's tests, forb content on MB was significantly higher than HF, but similar to MC, for all cuttings except June 30 (p=0.056) when the 3 sites did not differ. MC and HF formed homogeneous subsets for all cuttings except June 30, but differences were close to significance (α=0.05) for June 15 (p=0.068) and July 30 (p=0.061). Higher values for HF forb content in 1996 probably resulted from sampling only two grids within HF, one of which, Station, had the highest forb content of all HF grids sampled in 1995. Neither grazing (F= 0.002, p=0.96) nor burning (F=0.65, p=0.43) appeared to affect percentage of forbs present.

Forbs and grasses differed in their relative quality and both varied seasonally. Crude protein content of grasses (Table 2.6) and forbs (Table 2.7) on HF declined throughout each summer, especially in May and June. As indicated by the last two 1995 and last three 1996 cuttings, protein content usually increased on MC and MB after commencement of grazing. In the 1996 grazing trial, crude protein of forbs (F=11.36, p=0.004) and grasses (F=6.63, p=0.015) was greater in non-exclosure (grazed) samples. Grasses on burned sites were higher (F=8.94, p=0.01) in crude protein than on unburned sites, but large differences evident for first cuttings narrowed as summer progressed. Patterns were similar for forbs, but differences were not significant (F=0.24, p=0.66). When forb and grass samples from all sites were compared, crude protein content of forbs was higher than grasses in 1995 (F=183.47, p<0.001) and 1996 (F=59.14, p<0.001).

Unlike other variables, there was little seasonal variation in gross energy values (Table 2.8). Forbs and grasses had similar (F=1.47, p=0.23) gross energy content throughout 1995 on all three sites. Gross energy content of 1996 samples was not measured because of this low variation observed in 1995.

In contrast to gross energy, digestibility showed differences and seasonal patterns similar to crude protein. HF samples generally declined throughout summer by 10 to 33%; the seasonal decline in MC and MB digestibility values that occurred in both years usually slowed or stopped after cattle grazing began (Tables 2.9 & 2.10). The apparent influence of cattle grazing on digestibility was confirmed by results from the 1996 grazing trial; forbs (F=8.57, p=0.01) and grasses (F=6.81, p=0.014) from grazed sites were more digestible than plants from ungrazed sites. On burned sites, grasses were higher (F=35.08, p=<0.001) in digestibility than on unburned sites, but forbs did not differ between treatments (F=1.67, p=0.29). Overall, forbs were significantly more digestible than grasses in both 1995 (F=854.59, p<0.001) and 1996 (F=317.83, p<0.001).

Remaining comparisons used combinations of the variables that were directly measured, crude protein, gross energy, digestibility and biomass. Digestible protein (Appendices B.2 & B.3) and digestible energy (Appendix B.4) give estimates of amounts of protein and energy in forbs and grasses that were useable by ground squirrels. Patterns of seasonal variation in both did not change markedly because those patterns reflected patterns of variation in the original variables. However, in some cases the magnitude of differences between sites and treatments was affected. Means used in figures are the average of all cuttings from each treatment within each year, but statistical values cited are for repeated measures ANOVAs. In the 1996 grazing trial (Figure 2.3), grasses from grazed sites had increased digestible protein (F=6.27, p=0.02) compared to grasses from ungrazed sites; forbs also differed (F=8.99, p=0.02) between treatments. Burning did not affect all plants similarly (Figure 2.4); grasses from burned sites had greater levels (F=25.34, p<0.001) of digestible protein than grasses from unburned sites, but forbs were unaffected (F=0.59, p=0.49). Digestible protein content of forbs was higher than for grasses in 1995 (Figure 2.5: F=397.34, p<0.001) and 1996 (Figure 2.6: F=202.88, p<0.001). Digestible energy content (Figure 2.7) was higher for forbs than for grasses (F=1131.5, p<0.001), but this was due solely to variation in digestibility because differences in gross energy were non-significant.

Total digestible protein (Appendices B.5 & B.6) and total digestible energy (Appendix B.7) indicate availability of nutrients because they incorporate both quantity and quality. Previously described patterns of differences between forbs and grasses changed with these variables due to opposing trends for quality and biomass. Total digestible protein of grasses (F=62.13, p=0.001) and forbs (F=39.63, p<0.001) was greater on ungrazed sites as a result of increased biomass. Although differences were not significant (F=1.30, p=0.27), grass from burned areas generally provided more total digestible protein than grasses from unburned areas due to greater protein content and digestibility; no trend was apparent for forbs (F=0.05, p=0.83). Comparisons between forbs and grasses indicated greater amounts of digestible protein (1995: F=155.24, p<0.001, 1996: F=65.65, p<0.001) and digestible energy (F=285.02, p<0.001) from grasses; larger amounts of grass biomass offset higher values for protein content and digestibility of forbs.

Interactions between crude protein, gross energy, digestibility and biomass could increase the difficulty of determining the independent effects of these variables on growth of juvenile ground squirrels, which was a goal of this study. Correlations (Appendix B.8) were assessed to determine if more detailed study of the relationships between quality indicators was necessary. Positive correlations between crude protein and digestibility occurred in 1995 and 1996 for both forbs and grasses. Gross energy was also positively correlated with crude protein, but only for grasses. Biomass was not correlated with gross energy, but was generally negatively associated with crude protein. Negative correlations were also evident for digestibility and biomass except for forbs collected in 1995.

Discussion

Differences in squirrel traits among MC, MB and HF appear to be influenced by age and, to a lesser extent, by reproductive status. HF juveniles and reproductive females gained weight more slowly than comparable squirrels on MB and MC whereas other groups of squirrels did not differ between sites. For juveniles, differences in growth appeared to affect survival rates.

HF juveniles had lower survival rates than MC and MB juveniles, but these were probably not due to increased costs of hibernation. Young (1990) found no differences in costs of hibernation between juveniles and adult females based on similarities in total time in hibernation and time spent euthermic. Survival rates of females were similar on all three sites suggesting costs of hibernation did not differ for females. Therefore, hibernation costs to juveniles probably do not differ between sites. However, HF juveniles may not be as well prepared for hibernation as MC and MB juveniles. Heavier juveniles have a greater chance of surviving hibernation than lighter juveniles (Murie & Boag 1984); perhaps fewer HF juveniles reach weights necessary to survive hibernation.

In this study, weights were assumed to indicate body condition of individuals, particularly amount of body fat. Dobson (1992) found a strong correlation between body mass and condition for adults, but this correlation was weaker for actively growing individuals. However, squirrels used in Dobson's study were captured in mid-summer, over one and a half months before hibernation. Juvenile Belding's ground squirrels (Spermophilus beldingi) captured well in advance of hibernation may be relatively low in fat reserves (Bachman 1994) whereas juveniles captured just prior to hibernation have large fat reserves (Morton et al. 1974). Prehibernatory weights of juvenile Columbian ground squirrels probably reflect their fat reserves and, as a result, their ability to survive hibernation.

HF juveniles grew more slowly and probably reached lower prehibernation weights than MC and MB juveniles, likely as a result of lower food quality on HF. Lack of differences within other age categories suggests that effects of variation in food quality depend upon squirrel age. Although they do not grow as rapidly as juveniles, yearlings also experience large increases in size during summer (Boag & Murie 1981a) and are probably closer to juveniles than adults in terms of growth requirements (Kenagy et al. 1989). Lack of intersite differences for yearlings of either gender suggests that the age effect disappears after the first hibernatory period. However, weight gain of some adult squirrels differs among sites indicating that reproductive status as well as age should be considered when assessing relationships between squirrel traits and food quality.

Adult male Columbian ground squirrels have seasonal weight patterns similar to other ground squirrels (Rickart 1982, Kenagy et al. 1989, Michener & Locklear 1990). Periods of rapid weight loss during the breeding season are followed by intervals of increasing weight gain until it peaks in mid-summer. This is followed by a short period of slower weight gain and, in some cases, small loss of weight before hibernation. HF males do not recover lost weight as rapidly as males on MB and MC. The most noticeable differences were concurrent with the mid-summer declines in HF forage quality suggesting that variation in food quality can have a more pronounced effect if it coincides with critical periods for weight gain in the male annual cycle.

For adult females, reproduction affects the relationship between weight change and food quality, possibly because the timing of peak nutritional requirements differ for reproductive and non-reproductive females. Non-reproductive females accumulate most of the fat reserves necessary to survive hibernation (Bachman 1994) early in the growing season when food quality is high whereas reproductive females must recover lost weight during periods of lower food quality. Reproductive HF females recovered lost weight more slowly than comparable females on MB and MC; this was concurrent with periods of greater disparity in forage quality between sites. Declining forage quality may have a more pronounced effect on reproductive females than on non-reproductive females due to larger differences between nutritional requirements and food quality during the fattening period.

Growth of juveniles may be affected by timing of physiological demands and variation in food quality. All juveniles probably attempt to maximize growth throughout their active period (Koeppl & Hoffmann 1981), but growth of HF juveniles peaked in the first two weeks whereas MC and MB juveniles did not reach peak growth rates until the third and fourth week after emergence. This suggests that declining food quality on HF relative to MC and MB may limit the length of time during which HF juveniles can maximize growth. Juvenile nutritional requirements differ from those of adults based on differing physiological demands. Juveniles are growing structurally and have greater protein demands (White 1978) than do adults that are fattening and trying to maximize energy intake (Ritchie 1990). Both timing of peak food quality and nutritional requirements of squirrels must be taken into account when relating specific forage variables to ground squirrel growth.

If large differences occur between nutritional requirements and the amount of nutrients available in their food supply, squirrels may attempt to compensate behaviorally to reduce this disparity. Compensation could occur by selective foraging (Ritchie 1990) or by extending the active season (Dobson et al. 1992). Low forb biomass on HF may reduce the potential for compensation via selective foraging, but more squirrels seen on HF late in summer (pers. obs.) suggests that HF squirrels have an extended active season. The ability of adult ground squirrels to compensate for differences in food quality may account for the similarity in survivorship, weaning rates, and litter sizes between HF and other sites.

HF juveniles may also compensate for food quality differences by extending their active season, but this is unlikely to be an effective strategy for increasing prehibernatory weight given continuing declines in forage quality on HF and stricter nutritional constraints than for adults (White 1978, Hume et al. 1993). Based on growth rates to maximum weight, HF juveniles would have to extend their active season by ≅50% (3 more weeks) to achieve prehibernatory weights similar to MC and MB juveniles. An increase of that proportion would be outside the range of variation previously reported for juveniles (Dobson et al. 1992). Compensation of this type also assumes that HF juveniles could maintain growth at observed rates despite declining food quality. HF juveniles are probably not able to compensate for food quality differences; this conclusion is supported by the low survivorship of HF juveniles relative to MC and MB juveniles.

Food quality variation does not have an equal effect on all groups of squirrels. Greater disparity among sites observed for growth and survival of juveniles compared to weight gain and survival of adults suggests that variation in food quality has more pronounced effects on juveniles than on adults. Accounting for this difference is a necessary component of any explanation of food quality effects, hence I stress the effects of food quality variation on juveniles throughout the discussion of food quality indicators.

Evaluating the explanatory power of forage variables is based on determining the degree to which they explain observed differences in life history traits of forage consumers, both between and within sites (Bergeron & Jodoin 1987). In this study, determining the relative importance of the forage quality indicators involves assessing how well each forage variable meets the following conditions.

1) Forage quality indicator should differ between sites that differ in life history traits of ground squirrels.
2) Forage quality indicator should be correlated with known nutritional constraints of ground squirrels.
3) If the magnitude of intersite differences in life history traits varies based on differing nutritional requirements related to age, sex or reproductive status, then the pattern of food quality variation should be consistent with those differences.

Plant biomass has limited explanatory power in most ground squirrel studies because it simply indicates quantity with no direct indication of quality. Although reduced biomass can limit populations (Boutin 1990), Kilgore and Armitage (1978) found that populations of another sciurid, Marmota flaviventris, only consumed 0.8 to 3.0% of available plant biomass and plant biomass on all sites is much higher than maximum requirements of ground squirrels (Belovsky 1986). In fact, biomass and other measures reflecting quantity (total digestible energy and total digestible protein) were higher on HF.

Although total plant biomass does not explain intersite differences, its composition (i.e. forb content) is a better predictor. Columbian ground squirrels prefer forbs over grasses (Lambeth & Hironaka 1982, Harestad 1986, Andrusiak & Harestad 1989), but these studies did not examine which food quality factors are the basis of this preference. Ritchie (1988) found that optimal diets of S. columbianus usually contained more forbs than grasses; forbs and grasses differed in digestible energy content, but other quality indicators were not examined. Understanding why forbs are a better food source than grasses requires examination of more components of food quality.

Gross energy is a poor indicator of plant quality for ground squirrels. Variation within seasons and between plant groups is low, so foraging decisions based on maximizing gross energy yield only small increases in energy intake. More importantly, differences in gross energy content do not account for either lower growth rates of HF juveniles or slower recovery of lost weight in HF adults.

Differences in squirrel growth are reflected in estimates of energy content only when both gross energy and digestibility are combined. Given the higher forb content on MB and MC and more digestible energy in forbs than grasses, and declines in digestible energy that are coincident with lower weight gains of squirrels, it appears that differences in digestible energy content affect growth rates of squirrels. However, variation in digestible energy appears to be primarily a function of variation in digestibility and, while energy intake is important for adults rebuilding fat reserves (Robbins 1993), protein intake (White 1978) and digestibility (Demment & Van Soest 1985) may be more important for small, growing individuals like juveniles.

Differences in crude protein content between forbs and grasses are consistent with intersite differences in growth of juvenile ground squirrels. Juveniles require high levels of crude protein (Robbins 1993) and MC and MB squirrels have access to more food that is high in crude protein because both sites have more forbs than HF. However, these data do not adequately explain weight differences in adults or lack of differences in weaning rates and litter sizes.

Reproductive females experience protein demands that peak during gestation and lactation (Robbins 1993); HF females had weight gains during gestation and lactation similar to MB and MC females, but did not recover lost weight as rapidly even though protein requirements declined after lactation. Lack of differences in weaning rates and litter sizes also suggest that lower crude protein levels on HF are not affecting females during gestation and lactation. Measures of female reproduction must be analyzed cautiously given the suggestion of King et al. (1991) that female weight at emergence is a good predictor of reproductive success; HF females could be in better condition at emergence allowing them to compensate for lower protein levels. However, this is unlikely given lower weight gains for HF females during the prehibernatory period. Crude protein content alone does not explain these differences among the three sites.

Crude protein content is frequently cited as the basis for foraging decisions (Millar & Zwickel 1972, Tyser & Moermond 1983, Andrusiak & Harestad 1989, Eshelman & Jenkins 1989), but other factors may be influential. Bergeron & Jodoin (1987) found that food preference of Microtus pennsylvanicus was not significantly correlated with crude protein. However, when ratios of protein to secondary compounds (tannins and phenolics) or to digestibility (acid detergent fiber or lignin) were used, relationships between food choice and protein became significant. Measures of digestibility obtained from the assay used in my study are correlated with acid detergent fiber, lignin and secondary compound content (Choo et al. 1981); combined with values for crude protein, they give estimates of digestible protein consistent with intersite differences in squirrel growth. Additionally, these estimates may have more explanatory power than estimates of digestible energy; Langvatn & Hanley (1993) used digestible protein rather than digestible energy in their study of red deer (Cervus elaphus) because it was a more sensitive measure of quality. However, the role of digestibility in determination of food quality needs to be examined further.

Small animals usually select higher quality food than larger animals either due to the requirements of a less efficient digestive system (Demment & Van Soest 1983) or because they require less foraging time to fill their gut and can afford to be selective (Verlinden & Wiley 1989). Regardless of the evolutionary basis of selection, highly digestible food is particularly important to small individuals given their high mass-specific metabolic rates and low absolute gut capacities (Hume 1989). Although these facts have usually been used to explain interspecific differences (Hume 1989), they are also relevant to intraspecific differences (Belovsky 1986).

Juveniles on HF have access to food that is lower in digestibility than the food available to MC and MB juveniles. This reduces their net energy and net protein intake by increasing turnover time and decreasing turnover rate in their digestive tract (Hume et al. 1993). Small size decreases digestive efficiency of all juveniles relative to adults, but the problem may be compounded for HF juveniles. They eat food that is steadily declining in digestibility at the same time MC and MB juveniles' food is stable or increasing in digestibility. Additionally, slower growth of HF juveniles also means capacity of their digestive tract is increasing more slowly than for MC and MB juveniles (Hume 1989). Increasing disparity in food digestibility, and in the digestive efficiency of HF juveniles compared to MB and MC juveniles may account for the earlier peak in growth rates observed for HF juveniles.

Lower digestibility could also affect HF adults, particularly as levels decline throughout summer. Increasing differences between digestibility of forbs and grasses and declining digestibility values on HF seems to explain greater numbers of intersite differences in squirrel growth later in summer better than other aspects of food quality. Another possibility is that, due to lower growth rates as juveniles, HF adults are smaller than MB and MC adults resulting in lower digestive capacity and poorer utilization of food (Hume et al. 1993). Indeed, post-lactation weights suggest that HF females are smaller than MC and MB females. Although mechanisms of interaction between food quality and animal growth are unclear in Columbian ground squirrels, digestibility appears to be an important determinant of food quality.

Other food quality factors have been suggested as constraints in diets of herbivores. Digestion inhibition by secondary compounds has been linked to diet choice (Bergeron & Jodoin 1987), but grasses are relatively low in secondary compounds (Belovsky 1986) and the digestibility assay used in this study partially accounts for effects of secondary compounds that are enzyme inhibitors (Choo et al. 1981). Concentrations of minerals such as sodium, potassium, and phosphorus (Christian 1988, Robbins 1993) have been cited as important in diet choice, but most plant species available to ground squirrels contain adequate amounts of these minerals (Karasov 1985). Water content is important in arid habitats (Karasov 1985), but is known to affect diet choice in sub-alpine regions only during periods of prolonged drought (Frase & Armitage 1989). Frank (1994) suggested that polyunsaturated fats play an important role in hibernation which leads to diet selection based on high levels of polyunsaturates. However, in this study, ground squirrels did not appear to have access to large quantities of plant seeds, the best source of polyunsaturates (Pennington 1993).

Examination of food supply differences in relation to variables measured for ground squirrels suggests that some variables such as biomass and gross energy are not very useful. However, positive correlations between crude protein, digestibility, and, in some cases, gross energy indicate a need for more controlled tests of relative importance of different forage quality variables. Tests of this type are described in chapters 3 and 4.

As in this study, previous studies indicated the potential for pronounced effects of habitat differences on Columbian ground squirrels. Dobson et al. (1992) found large differences in growth rates of juveniles between study sites that may have been the result of habitat differences. These effects could change if the structure of the plant community was altered (Bucyanayandi & Bergeron 1990). The plant community at HF may have changed and become more dissimilar from MB and MC over time. Boag & Murie (1981b) reported survival rates of HF juveniles of $\cong$38%, more than twice as high as the rates reported here. Perhaps differences in disturbance regimes among the three study sites explain differences in forage composition and quality.

Cattle grazing is the main source of disturbance that differs between HF, and MB and MC. Little grazing by domestic livestock has occurred on HF in the past 25 years (Murie pers. comm.); MC and MB are grazed every year beginning in late June. Grazing could have both long-term and seasonal effects. Higher forb content on MB and MC could be the result of intermediate levels of disturbance leading to a more diverse plant community (Tilman 1985); this would be a long-term process requiring different sampling methods to quantify. However, long-term changes in plant community structure towards lower quality species have been documented for habitats of other rodents (Bucyanayandi & Bergeron 1990). A study of grazing effects of domestic sheep on S. columbianus habitats found the largest populations of ground squirrels on sites exposed to median levels of grazing; these were also the sites with the most diverse plant communities (Lambeth & Hironaka 1982).

Cattle grazing also may have seasonal effects through stimulation of new plant growth (Bergeron & Jodoin 1993), which reverses declines in forage quality resulting from plant maturation (Burton et al. 1964, Goldberg et al. 1980), and through enhanced protein content due to fertilization (Boag & Wiggett 1994). Ground squirrels are attracted to areas of new growth resulting from either natural or anthropogenic disturbance (Slade & Balph 1974, Lambeth & Hironaka 1982, Tyser & Moermond 1983) probably due to increased quality, which can also result from grazing (Bergeron & Jodoin 1993). Forage quality increased on MC and MB after cattle grazing commenced and, on MB at least, squirrels appeared to feed more frequently in highly grazed areas (Murie pers. comm.).

Burning had less pronounced effects than grazing. Although controlled burns can encourage foraging by ground squirrels (Johnson & Smith 1977), changes in forage quality due to burning occur too early in summer to positively affect juvenile growth rates. Biomass recovered rapidly on burned sites and quality differences narrowed as summer passed. Enhancing forage quality for juvenile ground squirrels would require enough burning to alter plant communities; lack of change in forb content indicates one burn is insufficient for this purpose. Repeated burns have not occurred recently on MB and MC so, if disturbance has led to intersite differences, cattle grazing is the most likely agent.

Relationships between food quality and ground squirrel life history traits indicate that plant community structure, in particular forb content, and quality indicators, especially protein content and digestibility, are effective in explaining variation in ground squirrel traits. However, alternative explanations such as differences in predation risk need to be considered. Experimental food supplementation of HF ground squirrels is one approach that could be used to determine the role of food in explaining reduced growth rates of HF juveniles, and to clarify the importance of specific food quality indicators.

Literature Cited

Allen, S.E. (ed.). 1989. Chemical analysis of ecological materials. 2nd edition. Blackwell Scientific Publications, Oxford.

Allison, M and Borzucki, R. 1978. Cellulase methods for the efficient digestion of grasses and brassicas. J. Sci. Food Agric. 29:293-297.

Andrusiak, L.A. and Harestad, A.S. 1989. Feeding behavior and distance from burrows of Columbian ground squirrels. Can. J. Zool. 67:381-384.

Bachman, G.C. 1994. Food restriction effects on the body composition of free-living ground squirrels, Spermophilus beldingi. Physiol. Zool. 67:756-770.

Batzli, G.O. and Cole, F.R. 1979. Nutritional ecology of microtine rodents: digestibility of forage. J.Mamm. 60:740-750.

Belovsky, G.E. 1986. Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. Oecologia 70:35-52.

Bergeron, J.M. and Jodoin, L. 1987. Defining "high quality" food resources of herbivores: the case for meadow voles (Microtus pennsylvanicus). Oecologia 71:510-517.

_____. 1993. Intense grazing by voles (Microtus pennsylvanicus) and its effect on habitat quality. Can. J. Zool. 71:1823-1830.

Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Can. J. Zool. 68:203-220.

Boag, D.A. and Murie, J.O. 1981a. Weight in relation to sex, age, and season in Columbian ground squirrels (Sciuridae: Rodentia). Can. J. Zool. 59:999-1004.

_____. 1981b. Population ecology of Columbian ground squirrels in southwestern Alberta. Can. J. Zool. 59:2230-2240.

Boag, D.A. and Wiggett, D.R. 1994. The impact of foraging by Columbian ground squirrels, Spermophilus columbianus, on vegetation growing on patches fertilized by urine. Can. Field Nat. 108:282-287.

Bucyanayandi, J.D. and Bergeron, J.M. 1990. Effects of food quality on feeding patterns of meadow voles (Microtus pennsylvanicus) along a community gradient. J. Mamm. 71:390-396.

Burton, G.W., Knox, F.E. and Beardsley, D.W. 1964. Effect of age on the chemical composition, palatability and digestibility of grass leaves. Agron. J. 56:160-162.

Christian, D.P. 1988. Effects of dietary sodium and potassium on mineral balance in captive meadow voles (Microtus pennsylvanicus). Can. J. Zool. 67:168-177.

Choo, G.M., Waterman, P.G., McKey, D.B. and Gartlan, J.S. 1981. A simple enzyme assay for dry matter digestibility and its value in studying food selection by generalist herbivores. Oecologia 49:170-178.

Demment, M.W. and Van Soest, P.J. 1985. A nutritional explanation for body-size patterns of ruminant and nonruminant herbivores. Am. Nat. 125:641-672.

Dobson, F.S. 1988. The limits of phenotypic plasticity in life histories of Columbian ground squirrels. In M.S. Boyce (ed.), Evolution of life histories of mammals. Yale University Press, New Haven, Conn. pp. 193-210.

_____. 1992. Body mass, structural size, and life-history patterns of the Columbian ground squirrel. Am. Nat. 140:109-125.

Dobson, F.S., Badry, M.J. and Geddes, C. 1992. Seasonal activity and body mass of Columbian ground squirrels. Can. J. Zool. 70:1364-1368.

Dobson, F.S. and Kjelgaard, K.D. 1985a. The influence of food resources on population dynamics in Columbian ground squirrels. Can. J. Zool. 63:2095-2104.

_____. 1985b. The influence of food resources on life history in Columbian ground squirrels. Can. J. Zool. 63:2105-2109.

Elliott, C.L. and Flinders, J.T. 1985. Food habits of the Columbian ground squirrel, Spermophilus columbianus, in southcentral Idaho. Can. Field Nat. 99:327-330.

Eshelman, B.D. and Jenkins, S.H. 1989. Food selection by Belding's ground squirrels in relation to plant nutritional features. J. Mamm. 70:846-852.

Festa-Bianchet, M. 1981. Reproduction in yearling female Columbian ground squirrels (Spermophilus columbianus). Can. J. Zool. 59:1032-1035.

Festa-Bianchet, M. and King, W.J. 1984. Behavior and dispersal of yearling Columbian ground squirrels. Can. J. Zool. 62:161-167.

Frank, C.L. 1994. Polyunsaturate content and diet selection by ground squirrels (Spermophilus lateralis). Ecology 75:458-463.

Frase, B.A. and Armitage, K.B. 1989. Yellow-bellied marmots are generalist herbivores. Ethol. Ecol. Evol. 1:353-366.

Goldberg, M., Tabroff, N.R. and Tamarin, R.H. 1980. Nutrient variation in beach grass in relation to beach vole feeding. Ecology 61:1029-1033.

Harestad, A.S. 1986. Food habits of Columbian ground squirrels: a comparison of stomach and fecal samples. The Murrelet 67:75-78.

Hume, I.D. 1989. Optimal digestive strategies in mammalian herbivores. Physiol. Zool. 62:1145-1163.

Hume, I.D., Morgan, K.R. and Kenagy, G.J. 1993. Digesta retention and digestive performance in sciurid and microtine rodents: effects of hindgut morphology and body size. Physiol. Zool. 66:396-411.

Johnson, D.R. and Smith, G.W. 1977. Population ecology and habitat requirements of Townsend's ground squirrels. Snake River Birds of Prey Research Project Annual Report. U.S. Dep. Int., Bur. Land Manage., Boise, Idaho. pp.142-163.

Jones, D.I.H. and Hayward, M.V. 1975. The effect of pepsin pre-treatment of herbage on the prediction of dry matter digestibility from solubility in fungal cellulases. J. Sci. Food Agric. 26:711-718.

Karasov, W.H. 1985. Nutrient constraints in the feeding ecology of an omnivore in a seasonal environment. Oecologia 66:280-290.

Kenagy, G.J., Sharbaugh, S.M. and Nagy, K.A. 1989. Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. Oecologia 78:269-282.

Kilgore, D.L. and Armitage, K.B. 1978. Energetics of yellow-bellied marmot populations. Ecology 59:78 -88.

King, W.J., Festa-Bianchet, M. and Hatfield, S. 1991. Determinants of reproductive success in female Columbian ground squirrels. Oecologia 86:528-534.

Koeppl, J.W. and Hoffmann, R.S. 1981. Comparative postnatal growth of four ground squirrel species. J.Mamm. 62:41-57.

Lambeth, R. and Hironaka, M. 1982. Columbian ground squirrels in subalpine forest openings in central Idaho. J. Range Manage. 35:493-497.

Langtavn, R. and Hanley, T.A. 1993. Feeding-patch choice by red deer in relation to foraging efficiency. An experiment. Oecologia 95:164-170.

Leco Corp. 1992. Operator's manual, Model FP-428 nitrogen analyzer. Leco Corporation, St. Joseph, MI. pp. 7:1-5.

Michener, G.R. and Locklear, L. 1990. Differential costs of reproductive effort for male and female Richardson's ground squirrels. Ecology 71:855-868.

Millar, J.S. and Zwickel, F.C. 1972. Characteristics and ecological significance of hay piles of pikas. Mammalia 36:58-68.

Morton, M.L., Maxwell, C.S. and Wade, C.E. 1974. Body size, body composition, and behavior of juvenile Belding's ground squirrels. Great Basin Nat. Mem. 34:121-134.

Murie, J.O. and Boag, D.A. 1984. The relationship of body weight to overwinter survival in Columbian ground squirrels. J. Mamm. 65:688-690.

Murie, J.O. and Harris, M.A. 1982. Annual variation of spring emergence and breeding in Columbian ground squirrels (Spermophilus columbianus). J. Mamm. 63:431-439.

Pennington, J.A.T. (ed.). 1993. Bowes & Churches' food values of portions commonly used. J.B. Lippincott Co., Philadelphia. pp.484.

Rickart, E.A. 1982. Annual cycles of activity and body composition in Spermophilus townsendii mollis. Can. J. Zool. 60:3298-3306.

Ritchie, M.E. 1988. Individual variation in the ability of Columbian ground squirrels to select an optimal diet. Evol. Ecol. 5:232-252.

_____. 1990. Optimal foraging and fitness in Columbian ground squirrels. Oecologia 82:71-86.

Robbins, C.T. 1993. Wildlife feeding and nutrition. 2nd.ed. Academic Press Inc., San Diego. pp.352.

Slade, N.A. and Balph, D.F. 1974. Population ecology of Uinta ground squirrels. Ecology 55:989-1003.

SPSS User's guide. 1996. SPSS Inc., Chicago, Ill. pp. 577.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. Am. Nat. 125: 827-852.

Tyser, R.W. and Moermond, T.C. 1983. Foraging behavior in two species of different-sized sciurids. Am. Midl. Nat. 109:240-245.

Verlinden, C. and Wiley, R.H. 1989. The constraints of digestive rate: an alternative model of diet selection. Evol. Ecol. 3:264-273.

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

Wiggett, D.R. and Boag, D.A. 1986. Establishing colonies of squirrels during their active season. Wildl. Soc. Bull. 14:228-290.

Young, P.J. 1990. Hibernating patterns of free-ranging Columbian ground squirrels. Oecologia 83:504 -511.

Zar, J.H. 1984. Biostatistical analysis. 2nd edition. Prentice-Hall Inc., Englewood Cliffs, N.J. 718 pp.

Figure 2.1. Map of ground squirrel study sites.

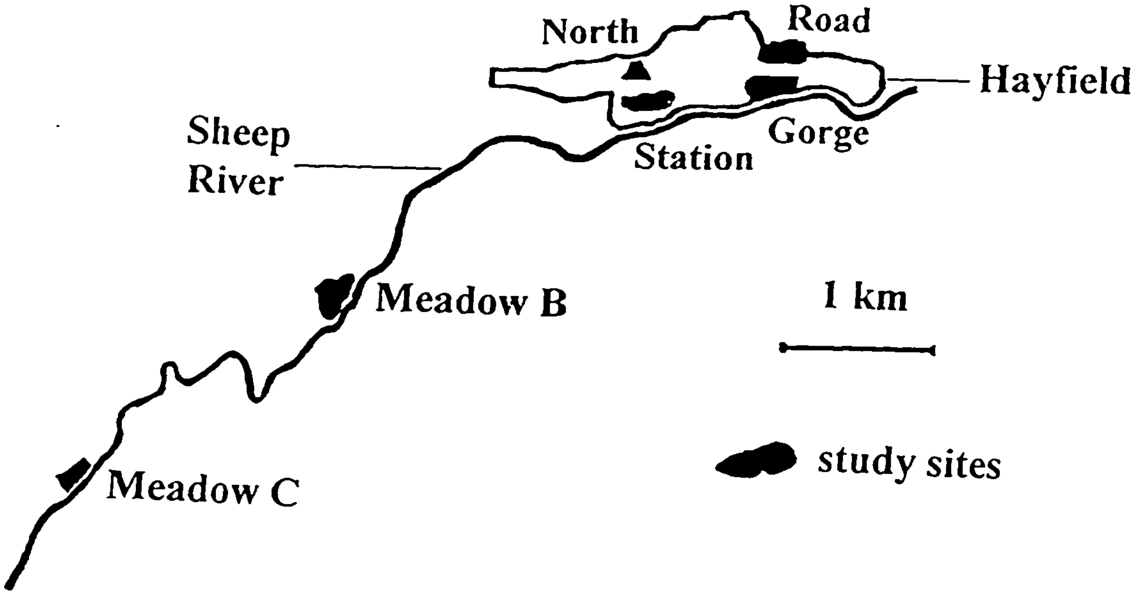

Figure 2.2. Mean (+1 S.E.) growth rates of juvenile ground squirrels on MC, MB and HF. Growth rates were calculated for successive two-week intervals after juveniles emerged from natal burrows. Data were pooled for 1995 and 1996.

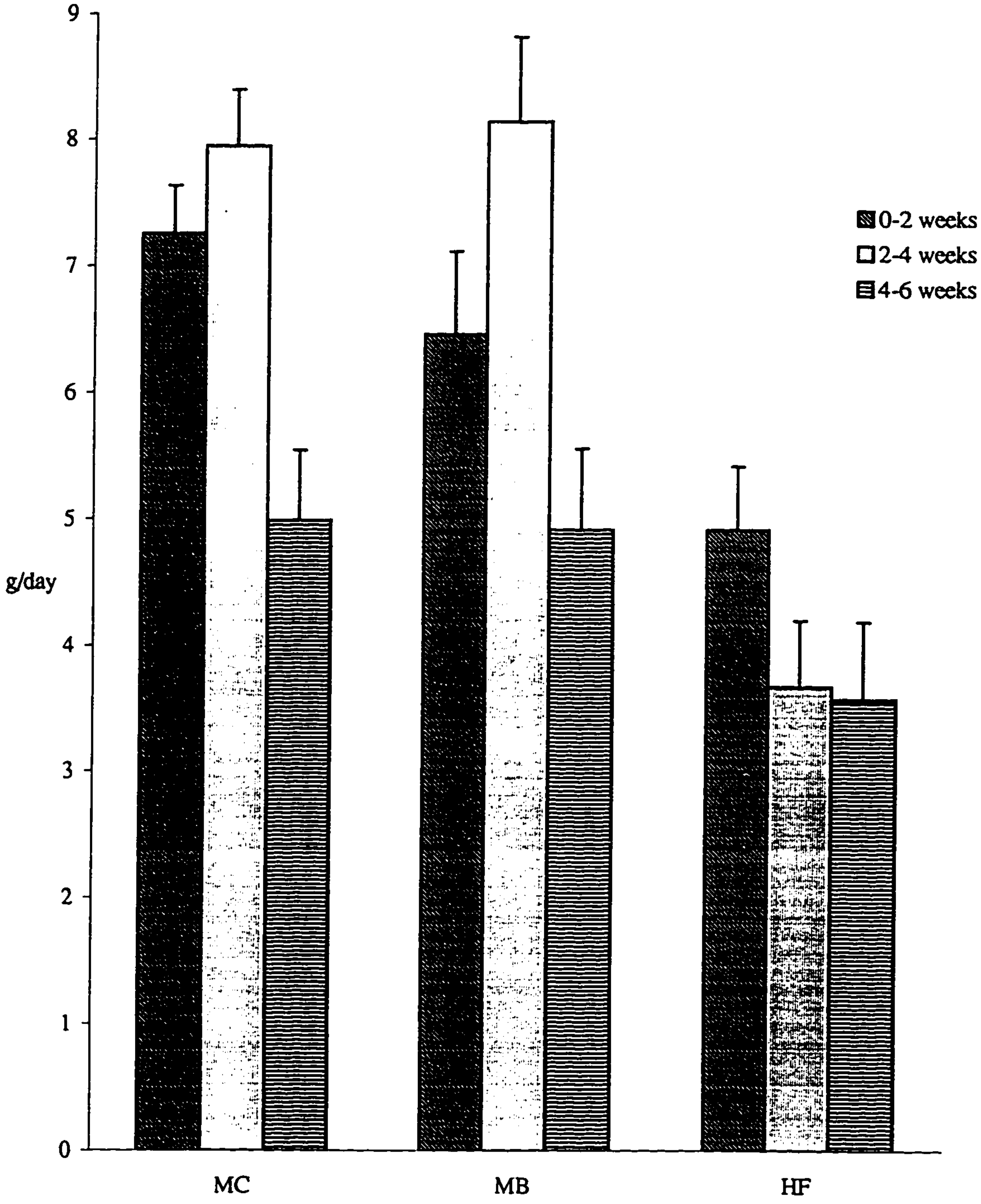

Figure 2.3. Mean (+1 S.E.) digestible protein content of forbs and grasses from MB and MC for samples protected from grazing by wire exclosures and for samples from grazed areas. Samples collected biweekly from July 15 to August 14/96.

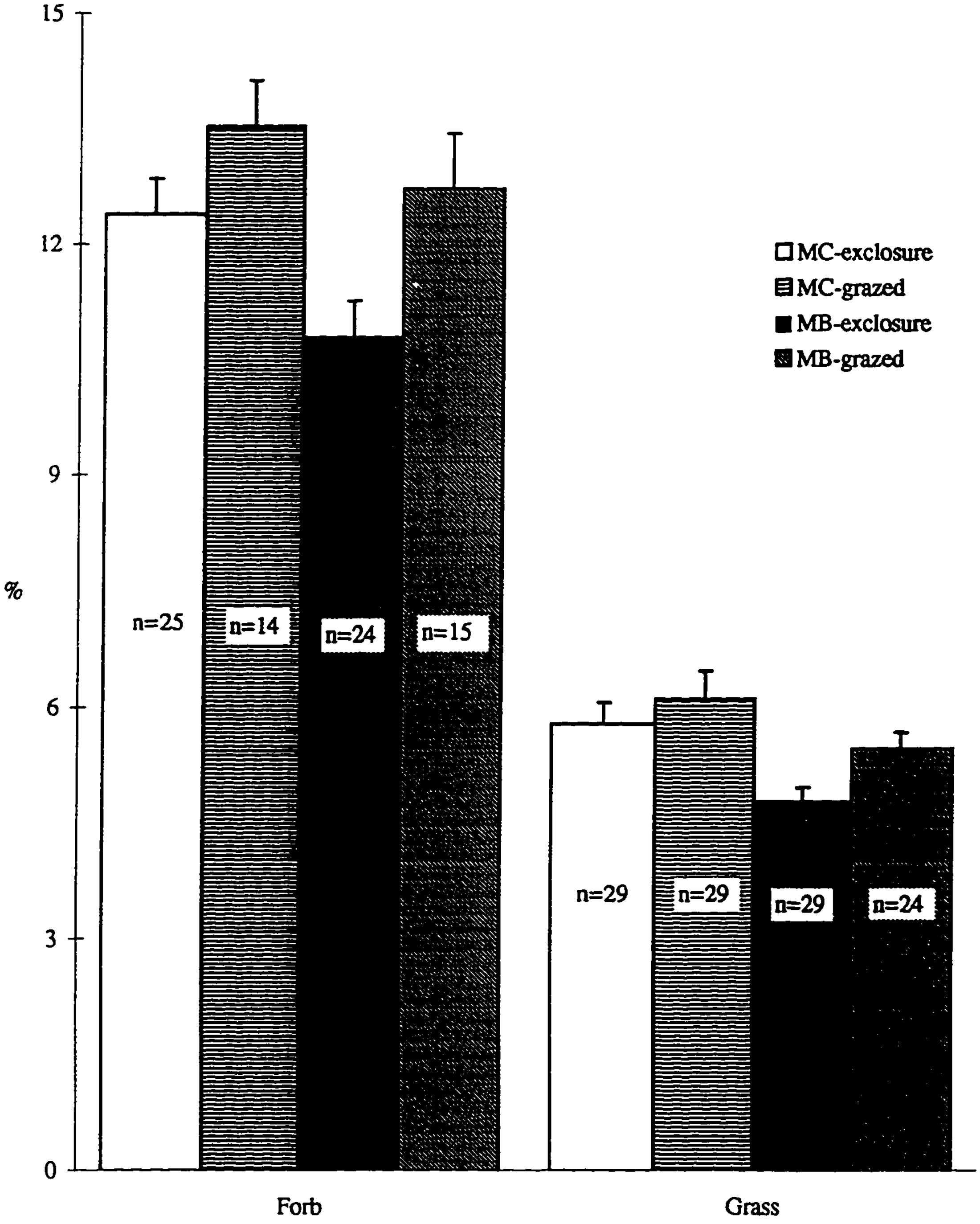

Figure 2.4. Mean (+1 S.E.) digestible protein content of forbs and grasses from unburned and burned areas on HF. Samples collected from June 2 to August 14, 1996.

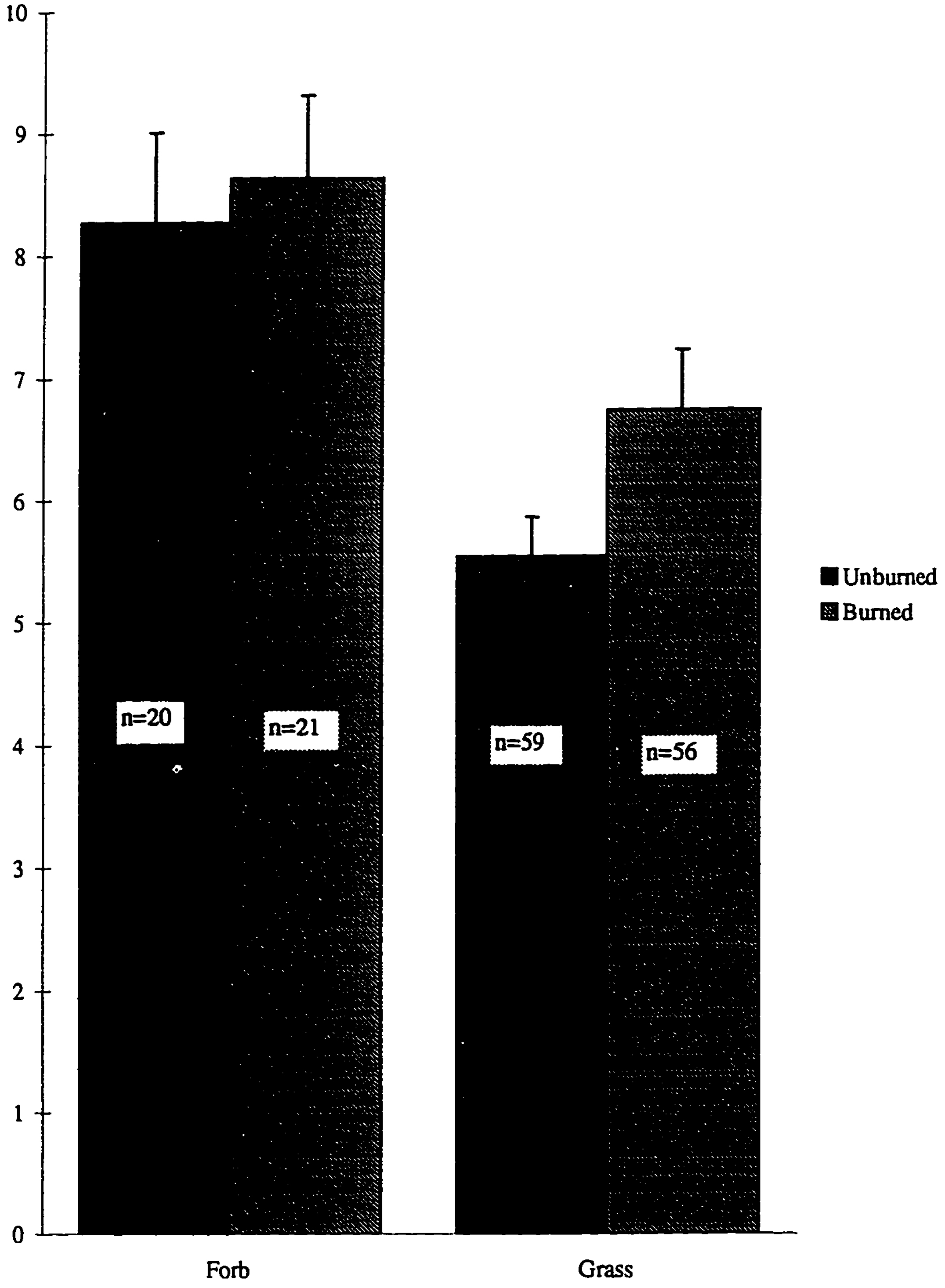

Figure 2.5. Mean (+1 S.E.) digestible protein content of forbs and grasses from MC, MB and HF for combined samples collected biweekly from May 31 to August 14, 1995.

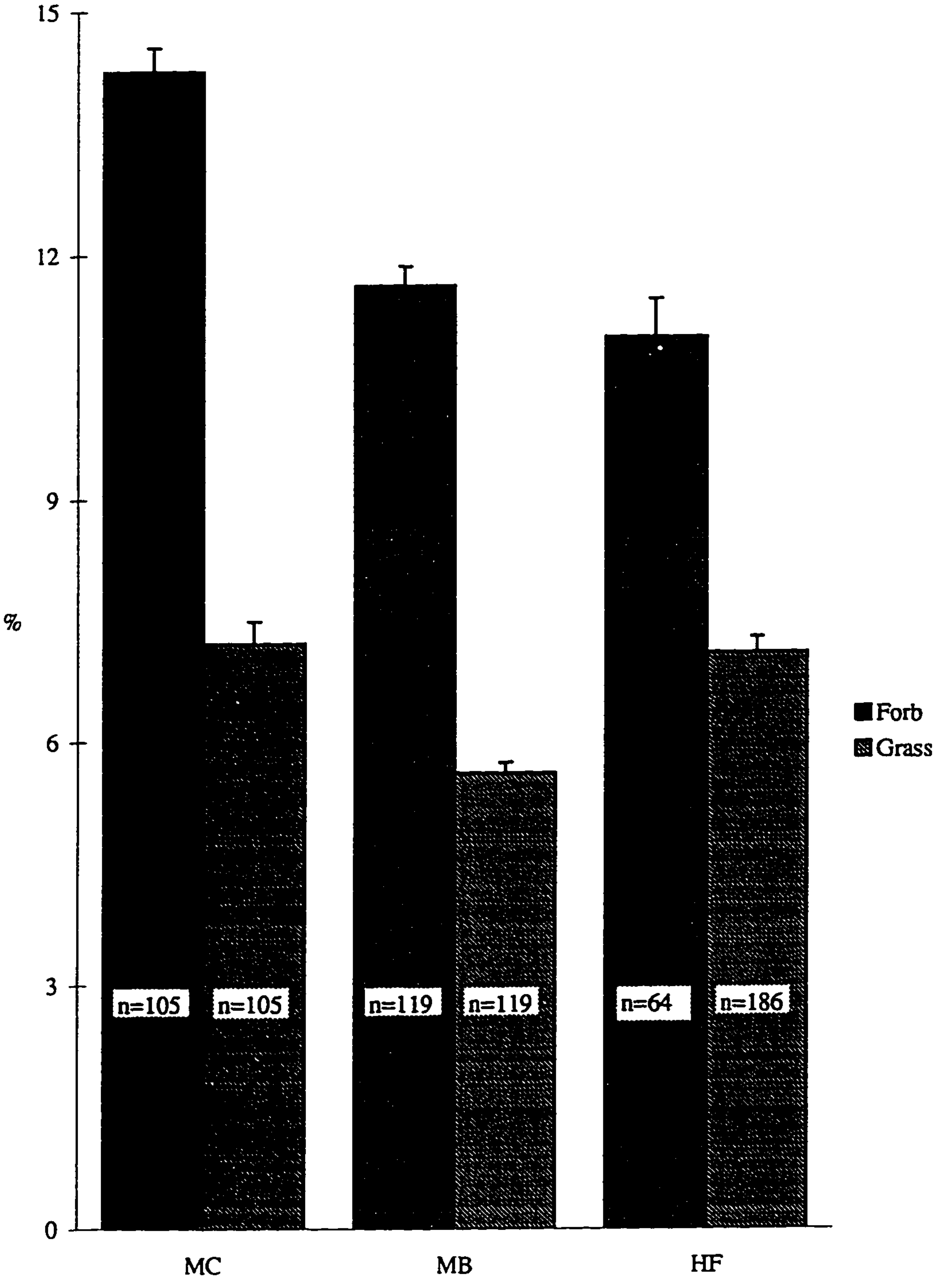

Figure 2.6. Mean (+1 S.E.) digestible protein content of forbs and grasses from MC, MB and HF for combined samples collected biweekly from May 31 to August 14, 1996.

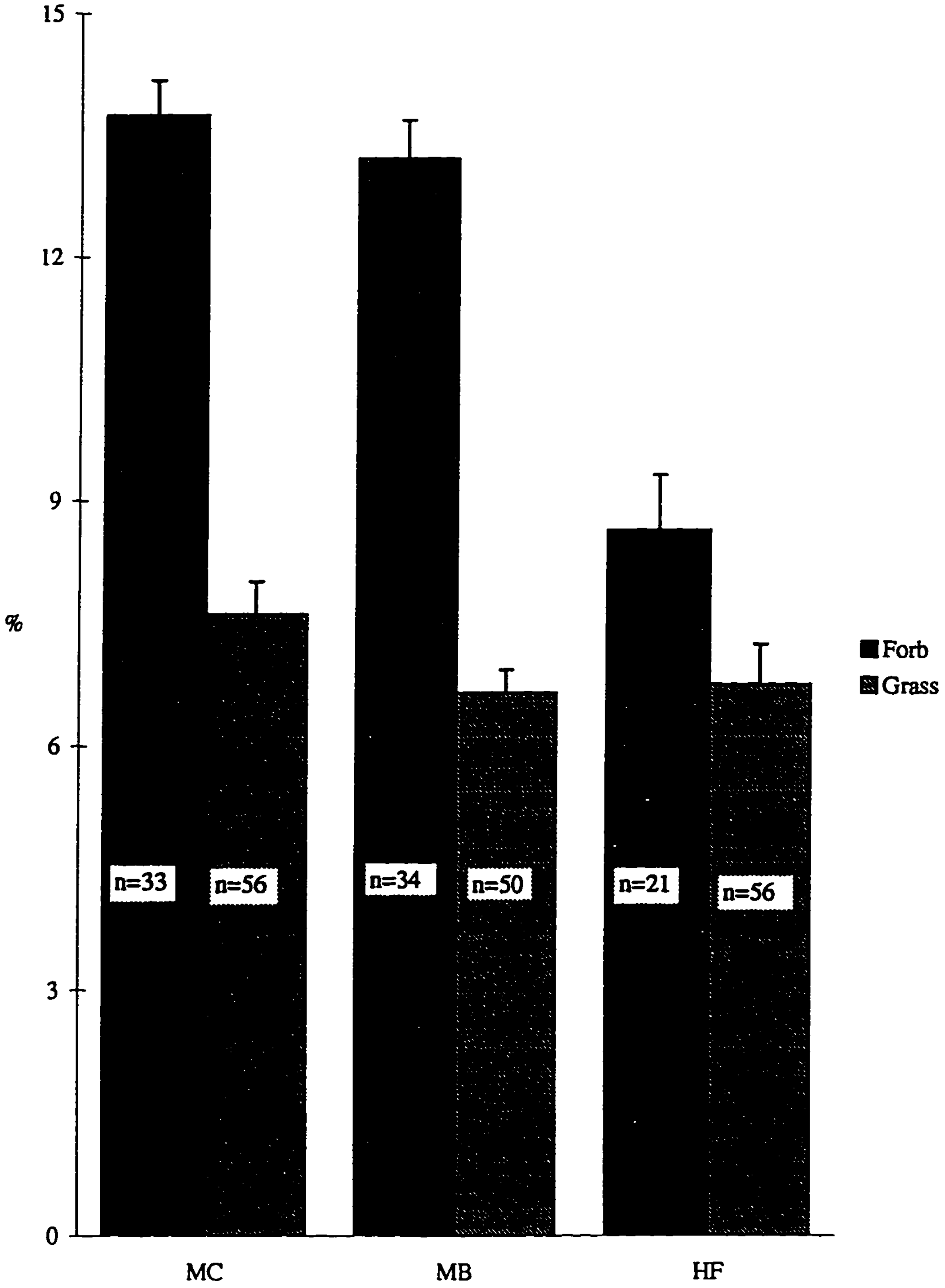

Figure 2.7. Mean (+1 S.E.) digestible energy content of forbs and grasses from MC, MB and HF for combined samples collected biweekly from May 31 to August 14, 1995.

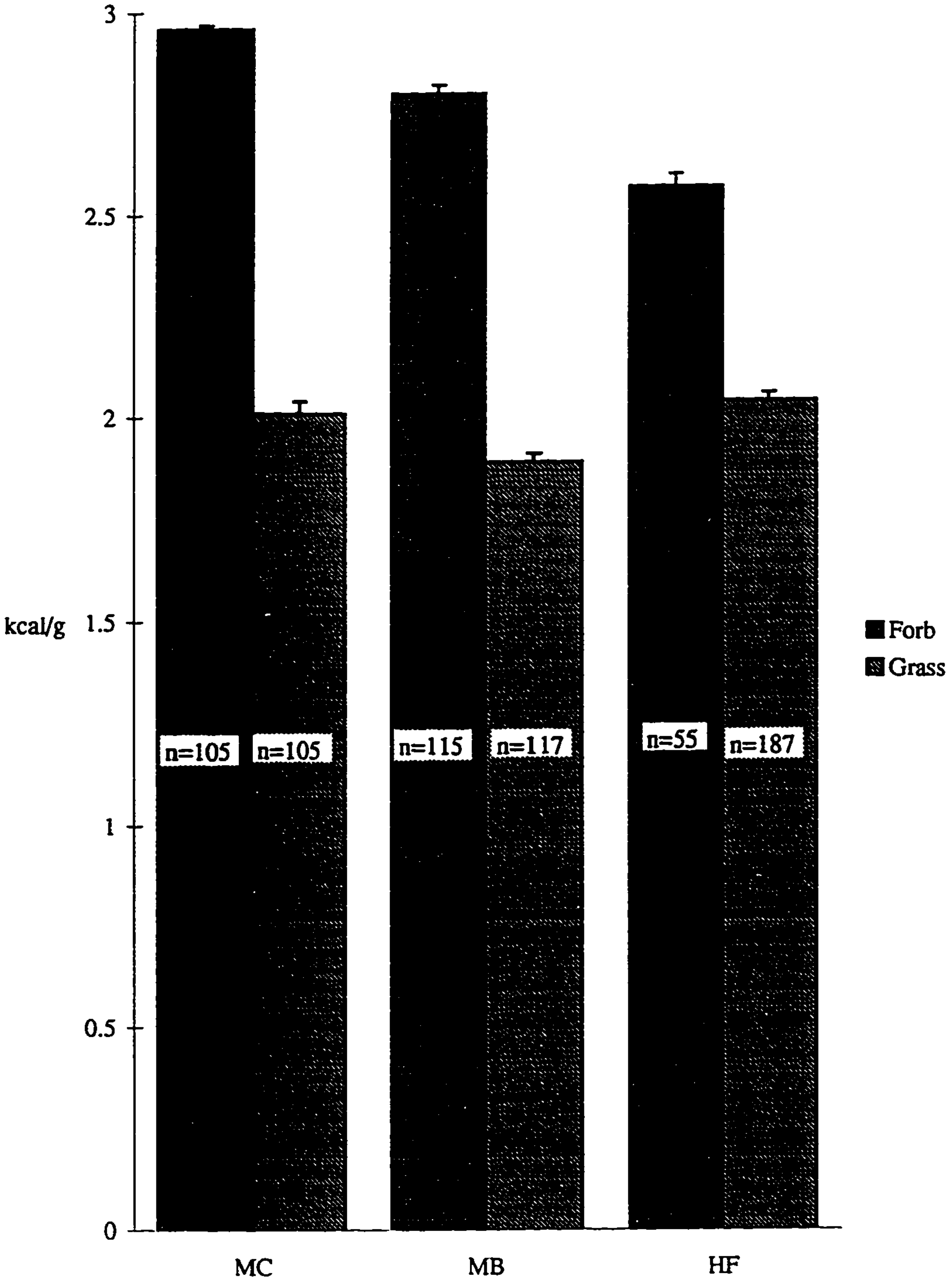

Table 2.1. Survival rates of juvenile and adult ground squirrels for 1995 and 1996. Juvenile survival rates were calculated by dividing the number of yearlings that emerged from hibernation in the spring by the total number of juveniles that emerged from natal burrows in the previous summer. Adult ground squirrel survival rates were determined by dividing the number of squirrels that emerged from hibernation by the number of squirrels present during the previous summer.

Year	Squirrel category	MC	MB	HF[a]
1995	Juveniles[b]	71%	77%	15%
		(34)[c]	(43)	(13)
1996	Juveniles	63%	68%	17%
		(24)	(44)	(42)
1995	Adult	89%	94%	67%
	females	(9)	(16)	(15)
1996	Adult	93%	82%	82%
	females	(14)	(22)	(34)
1995	Adult	57%	100%	85%
	males	(7)	(10)	(13)
1996	Adult	60%	69%	79%
	males	(10)	(13)	(24)

[a] HF data were obtained from one trapping grid in 1994. This grid was used in a supplementation experiment in 1995 and 1996 so combined data from two other grids were used for comparisons to MC and MB.

[b] Both sexes combined.

[c] Sample size.

Table 2.2. Mean weaning rates and mean litter sizes (±1S.E.) for 1995 and 1996. Weaning rates were calculated by dividing the number of females (yearlings excluded) that successfully raised juveniles to emergence by the number of females (yearlings excluded) still living on each site at the time of juvenile emergence. Mean litter sizes were calculated using only those females where proximity of the juveniles to the natal burrow or the female assured relatively high accuracy in determining litter size.

Year	MC		MB		HF	
	Weaning rate	Litter size	Weaning rate	Litter size	Weaning rate	Litter size
1995	69%	2.8	73%	3.0	59%	2.4
	(13)[a]	±0.2	(22)	±0.2	(32)	±0.2
		(9)		(15)		(17)
1996	44%	3.1[b]	36%	2.4[c]	46%	2.4
	(16)	±0.4	(25)	±0.4	(35)	±0.2
		(8)		(5)		(16)

[a] Sample size

[b] Excludes one yearling female that produced a litter of three juveniles.

[c] Excludes three litters of 3,4 and 4 respectively that were born and raised in captivity and one field-born litter of unknown size.

Table 2.3. Emergence weights (g) and growth rates (g/day) of juvenile ground squirrels for 1994, 1995 and 1996 (±1S.E.). Only emergence weights for juveniles captured within 4 days after emergence from their natal burrow were included. Growth rates were calculated for four different weight periods. Growth to maximum weight is the maximum weight reached by the juvenile minus its emergence weight divided by the total number of days in this interval. The remaining three growth rate values represent growth rates in the six weeks after each ground squirrel emerges from its natal burrow divided into separate two week intervals.

Year	Weight period	MC	MB	HF[a]
1994	Emergence	106.4 ±4.5 (18)[b]	112.6 ±2.4 (29)	103.8 ±2.4 (4)
1995	Emergence	106.3 ±4.6 (15)	106.3 ±2.6 (27)	101.3 ±3.9 (8)
1996	Emergence	109.2 ±6.1 (12)	105.7 ±12.5 (7)	120.5 ±4.4 (10)
1994	Maximum weight[c]	6.7 ±0.2 (15)	6.1 ±0.2 (29)	4.2 ±0.7 (5)
1995	Maximum weight	6.1 ±0.3 (16)	6.0 ±0.2 (27)	4.3 ±0.3 (8)
1996	Maximum weight	6.5 ±0.2 (9)	6.5 ±0.6 (6)	4.4 ±0.2 (16)
1995	First two weeks	6.8 ±0.3 (12)	6.1 ±0.3 (20)	4.5 ±0.5 (13)
1996	First two weeks	7.7 ±0.5 (12)	7.6 ±0.9 (7)	5.6 ±0.7 (7)
1995	Second two weeks	8.4 ±0.5 (11)	7.8 ±0.5 (8)	4.3 ±0.7 (7)
1996	Second two weeks	7.3 ±0.8 (8)	8.8 ±1.0 (4)	2.8 ±0.6 (5)
1995	Third two weeks	5.1 ±0.5 (11)	5.6 ±0.5 (8)	3.1 ±0.4 (5)
1996	Third two weeks	4.8 ±0.6 (8)	3.8 ±0.6 (5)	5.8 (1)

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[a] HF data were obtained from one trapping grid in 1994. This grid was used in a supplementation experiment in 1995 and 1996 so combined data from two other grids were used for comparisons to MC and MB.

[b] Sample size

[c] Only calculated for individuals that were recaptured and weighed at least 35 days after emergence from their natal burrow.

Table 2.4. Mean plant biomass (g/m^2) for successive cuttings in 1995 and 1996 (±1S.E.). All 1995 samples were collected within exclosures that had been in place for the previous two weeks. In 1996, exclosures were only used on MB and MC to simulate the absence of cattle grazing. These exclosures were in place for two, four and six weeks previous to cutting for the fourth, fifth and sixth cuttings respectively.

Cut date[a]	MC	MB	HF
May 31/95	**101.6** ±7.3 (20)[b]	**62.9** ±5.7 (20)	**57.9** ±6.6 (32)
June 15/95	**147.0** ±9.3 (20)	**72.0** ±5.3 (20)	**108.1** ±8.7 (32)
June 30/95	**221.6** ±14.9 (20)	**135.0** ±9.0 (20)	**170.5** ±12.8 (29)
July 15/95	**288.1** ±20.2 (13)	**130.0** ±9.4 (20)	**149.0** ±9.2 (32)
July 30/95	**137.7** ±13.2 (16)	**138.7** ±12.8 (19)	**166.6** ±7.9 (31)
August 14/95	**145.5** ±15.5 (16)	75.5±7.5 (20)	**219.1** ±11.6 (32)
Mean of all cuttings	**168.4** ±7.81 (105)	**102.1** ±4.55 (119)	**144.7** ±5.40 (188)

	Exclosure	No Exclosure	Exclosure	No Exclosure	Unburned	Burned[c]
May 31/96	n/a	**97.9** ±12.72 (10)	n/a	**36.0** ±6.25 (10)	**47.2** ±3.02 (10)	**17.6** ±2.59 (10)
June 15/96	n/a	**142.8** ±10.08 (10)	n/a	**115.0** ±17.15 (10)	**105.2** ±12.31 (10)	**106.9** ±18.87 (10)
June 30/96	n/a	**250.8** ±29.15 (10)	n/a	**146.2** ±16.08 (10)	**160.3** ±22.33 (10)	**145.3** ±21.86 (10)
July 15/96	**209.3** ±20.02 (10)	**92.2** ±11.44 (10)	**143.4** ±18.15 (10)	**47.5** ±5.91 (10)	**179.7** ±23.79 (10)	**210.9** ±27.84 (10)
July 30/96	**189.1** ±12.80 (10)	**76.4** ±9.94 (10)	**234.8** ±20.47 (10)	**86.0** ±5.97 (10)	**230.8** ±31.46 (10)	**218.7** ±27.31 (10)
August 14/96	**228.0** ±17.97 (9)	**38.6** ±6.56 (9)	**156.4** ±19.98 (9)	**29.5** ±3.91 (9)	**214.9** ±36.09 (10)	**251.4** ±28.33 (10)
Mean of all cuttings	**208.1** ±10.00 (29)	**177.8** ±10.69 (59)	**178.9** ±13.34 (29)	**77.5** ±7.04 (59)	**156.4** ±12.55 (60)	**158.5** ±13.67 (60)

[a] Median date of cuttings. Sites clipped on three successive days.

[b] Sample size

[c] HF sample points were distributed evenly amongst areas burned on April 29/96 and unburned areas.

Table 2.5. Mean forb content (%) of the biomass for successive cuttings in 1995 and 1996 (±1S.E.). All 1995 samples were collected within exclosures that had been in place for the previous two weeks. In 1996, exclosures were used only on MB and MC to simulate the absence of cattle grazing. These exclosures were in place for two, four and six weeks previous to cutting for the fourth, fifth and sixth cuttings respectively.

Cut date[a]	MC		MB		HF	
May 31/95	**22.6** ±2.3 (20)[b]		**23.3** ±3.8 (20)		**5.7** ±1.7 (32)	
June 15/95	**23.2** ±2.6 (20)		**35.0** ±5.0 (20)		**2.9** ±1.0 (32)	
June 30/95	**30.8** ±2.3 (20)		**26.3** ±2.7 (20)		**6.1** ±2.2 (29)	
July 15/95	**16.6** ±2.6 (13)		**28.2** ±3.9 (20)		**3.4** ±1.0 (32)	
July 30/95	**25.8** ±3.0 (16)		**20.7** ±3.8 (19)		**3.4** ±1.2 (31)	
August 14/95	**19.8** ±4.4 (16)		**23.9** ±4.4 (20)		**2.9** ±0.9 (32)	
Mean of all cuttings	**23.6** ±1.2 (105)		**26.3** ±1.6 (119)		**4.0** ±0.6 (188)	
	Exclosure	No Exclosure	Exclosure	No Exclosure	Unburned	Burned[c]
May 31/96	n\a	**17.4** ±4.3 (10)	n\a	**33.1** ±6.1 (10)	**8.7** ±5.4 (10)	**8.4** ±4.5 (10)
June 15/96	n/a	**20.5** ±5.2 (10)	n\a	**29.2** ±5.6 (10)	**12.4** ±6.6 (10)	**5.1** ±2.5 (10)
June 30/96	n/a	**24.6** ±6.8 (10)	n\a	**24.3** ±5.4 (10)	**12.8** ±4.2 (10)	**8.5** ±2.4 (10)
July 15/96	**21.8** ±4.9 (10)	**23.8** ±5.4 (10)	**26.1** ±7.2 (10)	**31.5** ±6.9 (10)	**11.8** ±5.5 (10)	**11.3** ±4.3 (10)
July 30/96	**25.7** ±6.3 (10)	**23.9** ±5.2 (10)	**27.4** ±5.6 (10)	**26.1** ±6.3 (10)	**15.0** ±7.2 (10)	**5.9** ±3.0 (10)
August 14/96	**18.7** ±5.7 (9)	**15.4** ±5.4 (9)	**35.5** ±6.4 (9)	**28.8** ±6.8 (9)	**10.5** ±6.6 (10)	**11.7** ±4.4 (10)
Mean of all cuttings	**22.2** ±3.2 (29)	**21.0** ±2.2 (59)	**29.4** ±3.7 (29)	**28.8** ±2.5 (59)	**11.9** ±2.4 (60)	**8.5** ±1.5 (60)

[a] Median date of cuttings. Sites clipped on three successive days.

[b] Sample size

[c] HF sample points were distributed evenly amongst areas burned on April 29/96 and unburned areas

Table 2.6. Mean crude protein content (%) of grasses for successive cuttings in 1995 and 1996 (±1S.E.). All 1995 samples were collected within exclosures that had been in place for the previous two weeks. In 1996, exclosures were used only on MB and MC to simulate the absence of cattle grazing. These exclosures were in place for two, four and six weeks previous to cutting for the fourth, fifth and sixth cuttings respectively.

Cut date[a]	MC	MB	HF
May31/95	**17.8** ±0.7 (20)[b]	**14.8** ±0.6 (20)	**19.7** ±0.5 (31)
June15/95	**14.3** ±0.5 (20)	**12.7** ±0.4 (20)	**15.3** ±0.6 (32)
June30/95	**12.1** ±0.4 (20)	**11.5** ±0.4 (20)	**13.6** ±0.4 (28)
July 15/95	**9.8** ±0.3 (13)	**11.0** ±0.4 (20)	**12.4** ±0.4 (32)
July 30/95	**14.0** ±1.0 (16)	**10.9** ±0.4 (19)	**12.2** ±0.4 (31)
Aug.14/95	**16.9** ±1.1 (16)	**12.2** ±0.5 (20)	**11.4** ±.0.3 (32)
Mean of all cuttings	**14.4** ±0.4 (105)	**12.2** ±0.2 (119)	**14.1** ±0.3 (186)

	Exclosure	No Exclosure	Exclosure	No Exclosure	Unburned	Burned[c]
May31/96	n/a	**18.6** ±1.5 (10)	n/a	**17.2** ±1.4 (6)	**15.8** ±1.0 (10)	**22.8** 1.4 (6)
June15/96	n/a	**14.0** ±0.7 (10)	n/a	**14.9** ±0.8 (10)	**13.8** ±.0.7 (10)	**14.7** ±0.6 (10)
June30/96	n/a	**11.8** ±0.8 (10)	n/a	**11.1** ±0.4 (10)	**10.6** ±0.7 (10)	**11.7** ±0.7 (10)
July 15/96	**11.6** ±0.6 (10)	**12.3** ±1.5 (10)	**11.9** ±0.6 (10)	**11.2** ±0.4 (7)	**9.5** ±0.5 (10)	**9.7** ±0.4 (10)
July 30/96	**12.3** ±1.0 (10)	**12.2** ±0.5 (9)	**10.3** ±0.4 (10)	**11.9** ±0.3 (10)	**8.4** ±0.4 (10)	**9.7** ±0.7 (10)
Aug.14/96	**13.0** ±1.2 (9)	**15.2** ±1.1 (7)	**10.7** ±0.6 (9)	**13.1** ±0.7 (7)	**8.4** ±0.3 (9)	**8.7** ±0.7 (10)
Mean of all cuttings	**12.3** ±0.5 (29)	**14.0** ±0.5 (56)	**11.0** ±0.3 (29)	**13.1** ±0.4 (50)	**11.1** ±0.4 (59)	**12.2** ±0.6 (56)

[a] Median date of cuttings. Sites clipped on three successive days.

[b] Sample size

[c] HF sample points were distributed evenly amongst areas burned on April 29/96 and unburned areas

Table 2.7. Mean crude protein content of forbs (%) for successive cuttings in 1995 and 1996 (±1S.E.). All 1995 samples were collected within exclosures that had been in place for the previous two weeks. In 1996, exclosures were used only on MB and MC to simulate the absence of cattle grazing. These exclosures were in place for two, four and six weeks previous to cutting for the fourth, fifth and sixth cuttings respectively.

Cut date[a]	MC		MB		HF	
May 31/95	**22.8** ±0.5 (20)[b]		**20.3** ±0.4 (20)		**21.3** ±0.5 (10)	
June 15/95	**18.2** ±0.4 (20)		**18.1** ±0.6 (20)		**19.5** ±2.7 (9)	
June 30/95	**16.2** ±0.5 (20)		**15.6** ±0.4 (20)		**16.6** ±2.3 (9)	
July 15/95	**14.7** ±0.5 (13)		**16.8** ±0.8 (20)		**16.0** ±1.1 (11)	
July 30/95	**20.7** ±0.6 (16)		**15.6** ±0.5 (19)		**16.9** ±1.3 (11)	
August 14/95	**23.1** ±0.7 (16)		**15.2** ±0.8 (20)		**14.0** ±0.8 (14)	
Mean of all cuttings	**19.4** ±0.4 (105)		**16.9** ±0.3 (119)		**17.1** ±0.7 (64)	
	Exclosure	No Exclosure	Exclosure	No Exclosure	Unburned	Burned[c]
May 31/96	n/a	**23.6** ±1.2 (5)	n/a	**21.8** ±1.2 (4)	**14.1** (1)	**20.5** (1)
June 15/96	n/a	**17.7** ±0.2 (6)	n/a	**18.5** ±1.0 (8)	**19.2** ±2.5 (3)	**18.6** ±0.1 (2)
June 30/96	n/a	**15.8** ±0.3 (8)	n/a	**16.4** ±0.6 (7)	**13.1** ±1.1 (5)	**15.2** ±1.0 (4)
July 15/96	**18.1** ±0.4 (9)	**18.9** ±1.3 (6)	**17.7** ±0.6 (10)	**18.0** ±1.8 (5)	**12.4** ±1.5 (3)	**13.0** ±1.6 (5)
July 30/96	**18.4** ±0.9 (9)	**19.4** ±0.8 (5)	**15.9** ±0.9 (9)	**17.6** ±0.8 (6)	**10.2** ±1.6 (5)	**10.7** ±0.7 (4)
August 14/96	**16.2** ±1.2 (7)	**18.6** ±1.3 (3)	**14.8** ±0.7 (9)	**18.8** ±2.2 (4)	**9.9** ±0.9 (3)	**9.9** ±0.8 (5)
Mean of all cuttings	**17.7** ±0.5 (25)	**18.7** ±0.5 (33)	**15.9** ±0.5 (28)	**18.3** ±0.5 (34)	**12.8** ±0.9 (20)	**13.1** ±0.8 (21)

[a] Median date of cuttings. Sites clipped on three successive days.

[b] Sample size

[c] HF sample points were distributed evenly amongst areas burned on April 29/96 and unburned areas.

Table 2.8. Mean gross energy content (kcal/g) of grasses and forbs for successive cuttings in 1995 (±1S.E.). All samples were collected within exclosures that had been in place for the previous two weeks.

Cutting date[a]	MC		MB		HF	
	Grass	Forb	Grass	Forb	Grass	Forb
May31	**4.15** ±0.02 (20)[b]	**4.16** ±0.02 (19)	**4.17** ±0.01 (19)	**4.09** ±0.04 (19)	**4.19** ±0.02 (31)	**3.99** ±0.03 (7)
June15	**4.12** ±0.03 (20)	**4.07** ±0.02 (20)	**4.13** ±0.02 (20)	**4.17** ±0.03 (18)	**4.11** ±0.02 (32)	**4.19** ±0.07 (7)
June30	**4.08** ±0.02 (20)	**4.00** ±0.01 (20)	**4.10** ±0.02 (20)	**4.16** ±0.03 (20)	**4.12** ±0.01 (29)	**4.22** ±0.05 (9)
July 15	**4.04** ±0.02 (13)	**3.97** ±0.02 (13)	**4.11** ±0.03 (20)	**4.15** ±0.03 (20)	**4.11** ±0.01 (32)	**4.17** ±0.06 (10)
July 30	**4.06** ±0.02 (15)	**4.04** ±0.02 (16)	**4.10** ±0.02 (19)	**4.13** ±0.03 (18)	**4.12** ±0.01 (31)	**4.07** ±0.03 (11)
August 14	**4.12** ±0.03 (16)	**4.04** ±0.03 (16)	**4.16** ±0.03 (19)	**4.12** ±0.05 (20)	**4.11** ±0.01 (32)	**4.03** ±0.04 (11)
Mean of all cuttings	**4.10** ±0.01 (104)	**4.05** ±0.01 (104)	**4.13** ±0.01 (117)	**4.14** ±0.02 (115)	**4.13** ±0.01 (187)	**4.12** ±0.03 (55)

[a] Median date of cuttings. Sites clipped on three successive days.

[b] Sample size

Table 2.9. Mean digestibility of grasses (%) for successive cuttings in 1995 and 1996 (±1S.E.). All 1995 samples were collected within exclosures that had been in place for the previous two weeks. In 1996, exclosures were used only on MB and MC to simulate the absence of cattle grazing. These exclosures were in place for two, four and six weeks previous to cutting for the fourth, fifth and sixth cuttings respectively.

Cut date[a]	MC		MB		HF	
May 31/95	**61.4** ±1.0 (10)[b]		**50.1** ±1.2 (10)		**57.5** ±1.1 (10)	
June 15/95	**48.8** ±0.8 (10)		**49.8** ±1.0 (10)		**55.8** ±1.6 (10)	
June 30/95	**42.1** ±0.6 (10)		**49.1** ±0.9 (10)		**48.2** ±1.2 (10)	
July 15/95	**43.0** ±0.5 (10)		**45.0** ±0.8 (10)		**43.7** ±0.7 (10)	
July 30/95	**44.6** ±1.6 (10)		**38.6** ±0.6 (10)		**46.0** ±1.1 (10)	
August 14/95	**51.4** ±1.1 (10)		**41.6** ±0.7 (10)		**45.2** ±0.9 (10)	
Mean of all cuttings	**48.5** ±0.9 (60)		**45.7** ±0.7 (60)		**49.4** ±0.8 (60)	
	Exclosure	No Exclosure	Exclosure	No Exclosure	Unburned	Burned[c]
May 31/96	n/a	**63.8** ±1.2 (10)	n/a	**57.8** ±1.0 (6)	**56.1** ±2.4 (8)	**66.7** ±1.1 (6)
June 15/96	n/a	**58.3** ±1.1 (10)	n/a	**54.2** ±1.1 (10)	**54.6** ±1.1 (10)	**60.2** ±0.9 (10)
June 30/96	n/a	**54.4** ±0.7 (10)	n/a	**53.9** ±0.6 (10)	**45.0** ±1.4 (6)	**54.9** ±1.3 (6)
July 15/96	**49.8** ±0.6 (10)	**48.1** ±1.4 (10)	**45.4** ±0.8 (10)	**46.5** ±0.5 (7)	**44.3** ±1.7 (8)	**48.4** ±0.8 (8)
July 30/96	**45.4** ±0.9 (10)	**45.3** ±1.0 (9)	**42.5** ±0.7 (10)	**41.8** ±0.7 (10)	**42.5** ±0.9 (8)	**47.3** ±1.1 (8)
August 14/96	**45.3** ±1.2 (9)	**47.3** ±1.0 (7)	**42.5** ±0.5 (9)	**48.1** ±1.4 (7)	**40.1** ±0.8 (6)	**46.1** ±1.5 (6)
Mean of all cuttings	**46.8** ±0.6 (29)	**53.3** ±1.0 (56)	**43.5** ±0.5 (29)	**50.1** ±0.9 (50)	**48.5** ±1.1 (46)	**54.0** ±1.2 (44)

[a] Median date of cuttings. Sites clipped on three successive days.

[b] Sample size

[c] HF sample points were distributed evenly amongst areas burned on April 29/96 and unburned areas.

Table 2.10. Mean digestibility of forbs (%) for successive cuttings in 1995 and 1996 (±1S.E.). All 1995 samples were collected within exclosures that had been in place for the previous two weeks. In 1996, exclosures were used only on MB and MC to simulate the absence of cattle grazing. These exclosures were in place for two, four and six weeks previous to cutting for the fourth, fifth and sixth cuttings respectively.

Cut date[a]	MC		MB		HF	
May 31/95	**72.8** ±1.5 (10)[b]		**72.3** ±1.1 (10)		**69.6** ±4.4 (5)	
June 15/95	**70.6** ±0.9 (10)		**70.9** ±1.1 (10)		**64.2** ±2.0 (4)	
June 30/95	**75.1** ±0.8 (10)		**63.5** ±1.2 (10)		**65.0** ±2.0 (5)	
July 15/95	**72.8** ±1.2 (9)		**67.2** ±1.7 (10)		**61.0** ±1.6 (5)	
July 30/95	**75.4** ±0.6 (10)		**67.8** ±1.5 (10)		**61.4** ±0.6 (5)	
August 14/95	**74.4** ±1.0 (10)		**67.6** ±0.8 (10)		**62.1** ±2.4 (5)	
Mean of all cuttings	**73.5** ±0.5 (59)		**68.2** ±0.6 (60)		**63.9** ±1.1 (29)	
	Exclosure	No Exclosure	Exclosure	No Exclosure	Unburned	Burned[c]
May 31/96	n/a	**75.3** ±0.7 (5)	n/a	**78.4** ±0.8 (4)	**55.18** (1)	**65.48** (1)
June 15/96	n/a	**74.9** ±0.6 (6)	n/a	**72.9** ±1.5 (8)	**67.8** ±6.6 (3)	**75.1** ±0.2 (2)
June 30/96	n/a	**75.4** ±1.1 (8)	n/a	**71.1** ±0.6 (7)	**65.7** ±2.3 (5)	**69.8** ±2.0 (4)
July 15/96	**71.4** ±1.1 (9)	**67.8** ±2.1 (6)	**70.0** ±1.2 (6)	**72.8** ±1.8 (5)	**66.0** ±2.9 (3)	**63.5** ±2.7 (5)
July 30/96	**70.4** ±1.2 (9)	**73.3** ±1.6 (5)	**66.0** ±1.5 (9)	**67.4** ±0.8 (6)	**60.2** ±1.9 (5)	**61.7** ±2.1 (3)
August 14/96	**66.3** ±2.9 (7)	**73.7** ±1.4 (3)	**67.4** ±1.3 (9)	**70.9** ±1.6 (3)	**63.7** ±5.4 (3)	**60.2** ±2.5 (5)
Mean of all cuttings	**69.6** ±1.1 (25)	**73.8** ±0.5 (33)	**67.5** ±0.8 (24)	**72.0** ±0.7 (33)	**63.8** ±1.6 (20)	**64.9** ±1.5 (20)

[a] Median date of cuttings. Sites clipped on three successive days.

[b] Sample size

[c] HF sample points were distributed evenly amongst areas burned on April 29/96 and unburned areas.

Chapter 3: Effects of Food Supplementation on Columbian Ground Squirrels With a "Poor Quality" Natural Food Supply

Introduction

Food quality is an important determinant of growth and survival of many species (Boutin 1990), but other factors can limit growth. Differences in predation risk can affect growth by limiting foraging time (Lima & Dill 1990). Differences in foraging ability can result in slower growth if poor quality food items are utilized (Ritchie 1991). These factors, and others (e.g. parasite loads), have the potential to explain observed differences in growth of Columbian ground squirrels. One method for gaining insight into the role food plays in determination of growth rates is food supplementation of study populations.

Dobson and Kjelgaard (1985a, 1985b) documented increased survival and reproduction when Columbian ground squirrels were given supplemental food. Although growth rates were not determined, juveniles had increased survival and increased weights after hibernation suggesting that growth the previous summer was enhanced by supplementation. If populations in which juveniles grow slowly and have low survivorship are food-limited, then food supplementation should increase growth and survival.

Supplementation effects observed by Dobson and Kjelgaard (1985a, 1985b) resulted from addition of food rich in both energy and protein. Supplementation positively affected all ages, sexes and reproductive groups so no information about differences in nutrient requirements of different squirrel groups was obtained. Supplementation of populations with food that is energy or protein limited could provide information about the relative importance of these major nutrients. Adding those types of food to Columbian ground squirrel colonies where growth rates are low will provide information about both the relationship of food in general to growth rates and the relative importance of protein and energy.

Monitoring of different ground squirrel populations in 1994 indicated that HF juveniles had lower rates of growth (≅50% lower) and survival (350 to 500% lower) than juveniles living in 2 other colonies in the same region (Chapter 2). Food quality on HF was lower than the other 2 sites suggesting that this factor limited growth of HF juveniles (Chapter 2). However, other factors could have negatively affected growth of HF juveniles. This chapter examines effects of experimental food supplementation on growth of HF ground squirrels. The importance of energy to ground squirrels was examined by using a food that was energy-rich, but similar in protein content (National Research Council 1982) to the natural food supply.

Methods

Study areas were the four sites on HF described in Chapter 2. Two sites, Station and Gorge, were supplemented with commercial livestock feed (rolled corn, Zea mays) from May 27 to August 16 in both 1995 and 1996. North and Road were not supplemented and served as controls. To begin supplementation, piles of corn were placed in areas where ground squirrels were concentrated (≅15 locations/grid) within supplemented sites. These areas were determined from trapping locations gathered during the pre-supplementation period. When juveniles emerged from natal burrows, additional piles (2-5 piles/grid) were placed near natal burrows that were not within 20 m of existing piles to ensure juveniles had access to corn. All piles were checked daily and replenished as necessary. A total of ≅500 kg of corn was added in each year.

Methods for trapping ground squirrels, and for determining gross energy and crude protein of corn are described in Chapter 2. Corn was obtained in 25 kg bags and one sample was taken from each bag in 1995 for food quality analyses. Because the pepsin-cellulase assay (Chapter 2) is unsuitable for measuring digestibility of seeds (Choo et al. 1981), published digestibility values for corn (National Research Council 1982) were used. Data analyses were similar to those described in Chapter 2. Grids were nested within treatment (supplemented or non-supplemented) for analyses where possible, but small sample sizes frequently necessitated pooling data within treatments.

Results

Although survival data are available for only one year, there was strong evidence that supplementation increased survivorship of juveniles ($G=32.99$, $p<0.001$, Table 3.1). As well, Gorge juveniles had a 15% survival rate in 1994 before supplementation (Chapter 2: Table 2.1) compared to a 56% survival rate after supplementation commenced. Neither adult male (G=0.25, p=0.62) nor adult female (G=0.18, p=0.68, Table 3.1) survival was affected by food addition.

There was some indication that supplementation enhanced female reproduction (Table 3.2), but this varied between years. Weaning rates were similar between treatments in 1995 (G=0.29, p=0.59), but supplemented females were more successful in weaning litters in 1996 (G=7.80, p=0.005). Supplementation appeared to affect the ability of yearling females to reproduce; four yearlings weaned litters on supplemented grids in 1996, whereas only two other cases were recorded from 1994 to 1996, both of which occurred on a non-HF grid, MC (Chapter 2).

Results from 1996 should be interpreted cautiously because heavy snowfall in early May of that year could have caused the reduction in weaning rate from 1995 to 1996 observed on North, which was an important factor in the occurrence of significant treatment effects in 1996. North females were probably more severely affected by these snowfalls than females on other HF sites because they emerged earlier (pers. obs.) and were at a more critical period (i.e. gestation) of their reproductive cycle than were later emerging females. However, Gorge females exhibited increased weaning rates after supplementation which suggests that there were beneficial effects of added food. Adverse spring weather may also have affected litter sizes of North females more than other HF females; North was the only HF grid on which litter sizes declined from 1995 to 1996 (Table 3.2). Differences between treatments were not significant in either year (1995: F=1.30, p=0.30, 1996: F=1.35, p=0.27), but the trend suggests that supplementation could have positively influenced litter sizes.

Weight change data from both years were frequently pooled because sample sizes were usually too small to allow for separate analyses. For all groups, supplemented squirrels gained weight more rapidly than did non-supplemented squirrels (Figure 3.1). Adult males (Appendix C.1) on supplemented grids gained weight more rapidly than non-supplemented males (F=12.35, p=0.003) with the greatest differences occurring in the first 30 to 45 days after supplementation commenced. Supplementation also appeared to increase weight gains of yearling males (Appendix C.2: F=12.13, p=0.01) and yearling females (Appendix C.3: F=45.57, p=0.001). Due to small sample sizes, it is difficult to comment on weight change patterns for either gender of yearlings. Supplemented non-reproductive adult females (Appendix C.4) gained weight significantly faster (F=25.46, p=0.001) than non-supplemented females with more pronounced differences in the first 30 to 45 days after supplementation began. Fewer recaptures, evident in smaller sample sizes, of supplemented females late in summer may be indicative of earlier hibernation than for non-supplemented females.

Despite small sample sizes and possibly differing stages of reproduction, treatment effects were close to significance (α=0.05) for reproductive females. Supplementation increased (F=5.02, p=0.052) weight gains of females that weaned juveniles (Appendix C.5) compared to non-supplemented reproductive females, but patterns of weight change were different from non-reproductive females. Supplementation appeared to have only minor effects on weight during the first 30 days after supplementation commenced, which corresponds roughly to the interval from late gestation to the end of lactation. Effects of supplementation were more obvious in the post-lactation period when reproductive females fed corn were able to gain weight more rapidly than non-supplemented reproductive females.

Effects of supplementation on adult females were also assessed by comparing spring emergence weights in 1996. Only first capture (range of first capture dates: April 23 to May 1) weights for females captured before May 2 were used because heavy snowfalls disrupted trapping schedules after this date. Supplemented females (Station: 492±10, n=12, Gorge: 481±18, n=8) emerged heavier (F=30.27, p<0.001) than non-supplemented females (North: 425±12, n=12, Road: 379±15, n=5). Only 2 yearling females were captured in this period so I was unable to make similar comparisons for this age group.

Supplementation of females during lactation did not appear to affect pre-weaning growth of their offspring. Juveniles (Table 3.3) from all HF sites had similar emergence weights in 1995 (F=0.31, p=0.61) and 1996 (F=0.58, p=0.45). However, once they emerged from natal burrows, supplemented juveniles grew faster than non-supplemented juveniles. Growth rates to maximum weight were 1.5 to 2 g/day higher for supplemented juveniles in both years (1995: F=15.83, p=0.003, 1996: F=23.90, p<0.001).

Biweekly growth rates also differed between treatments (Figure 3.2). Data from 1995 and 1996 for the two-week intervals were pooled because year was a non-significant factor (F=2.44, p=0.13). Supplemented juveniles grew faster than non-supplemented juveniles (F=18.22, p<0.001) with the largest differences occurring during the first four weeks after emergence; rates were more similar for the last two-week interval. Both treatments had similar growth patterns with peak growth rates in the first two weeks followed by declines in growth rates in subsequent intervals.

Gross energy content of corn was 4.13 kcal/g (S.E.= 0.01, n=17) and crude protein content was 8.0% (S.E.= 0.1, n=17). These data were combined with published values for digestibility of 75% (National Research Council 1982) to give values for digestible energy (3.10 kcal/g) and digestible protein (6.0%).

Discussion

Supplementation of HF squirrels produced many effects similar to those observed by Dobson & Kjelgaard (1985a, 1985b) in their food addition study. Survivorship was affected similarly; adult survival rates were unchanged and juvenile survivorship increased when squirrels were supplemented. These results are consistent with results of Chapter 2 indicating that higher quality natural food leads to greater survival of juveniles, but not adults.

Timing of supplementation may play an important role in determining the effects of food addition. Both this study and Dobson & Kjelgaard (1985a, 1985b) found higher weaning rates in the year after supplementation began. Dobson & Kjelgaard (1985a, 1985b) began supplementation after juveniles started emerging from natal burrows; thus added food would not have affected weaning rates that year. However, I began supplementation during late gestation so females had additional food during the most costly stage of reproduction, lactation (Glazier 1990). Despite the earlier addition of food, there was no effect on weaning rate. The delayed effect of supplementation suggests that nutrient intake during gestation and lactation is less important to reproduction than body condition at the beginning of gestation.

These results are consistent with other studies (King et al. 1991, Risch et al. 1995) that indicate spring emergence weights of females are good predictors of female reproductive success. Spring weights of supplemented females were higher in 1996 than for non-supplemented females, probably due to greater weight gain during the previous summer. Higher spring weights were probably also responsible for increased weaning rates of supplemented yearlings in 1996. Festa-Bianchet (1981) noted that reproduction by yearlings was infrequent, but when it occurred it was probably the result of elevated food quality. Availability of high quality food in the summer of 1995 increased reproduction by yearlings probably because supplemented yearlings grew faster as juveniles and were likely to be heavier than non-supplemented yearlings the next spring.

Unlike previous studies (Dobson & Kjelgaard 1985a, 1985b), litter sizes did not increase after supplementation, which may be due to differences in the time at which food addition commenced. Squirrels in the second year of Dobson & Kjelgaard's (1985a, 1985b) study were supplemented throughout gestation and litter sizes increased; I did not supplement during this period and litter sizes were unaffected. However, studies of female Belding's ground squirrels (Spermophilus beldingi) supplemented from early gestation to weaning show no effect on litter sizes (Trombulak 1991). Differing results between Dobson and Kjelgaard's (1985a, 1985b) study and Trombulak's (1991) study may be due to supplementation that occurred during the previous summer in one study (Dobson & Kjelgaard 1985a, 1985b), but not in the other (Trombulak 1991). The combined results of these studies support the earlier conclusion that condition at the beginning of gestation is more important to reproductive females than food quality during gestation and lactation.

While food addition may have influenced female reproductive success, it did not affect survival rates. Perhaps non-supplemented adult squirrels compensated for lower food quality by extending their active season (Dobson et al. 1992). Juveniles may also compensate by extending their active season, but this may not be sufficient to increase survival. In his study of Belding's ground squirrels, Trombulak (1991) found that some control juveniles remained active longer than supplemented juveniles and reached similar prehibernatory weights. Despite this, survival of supplemented juveniles was higher. Given declining rates of gain and food quality on HF (Chapter 2), it is unlikely that non-supplemented juveniles extend their active season long enough to reach prehibernatory weights similar to those of supplemented juveniles.

Ability to reach sufficient prehibernatory weights may be affected by maternal influences on emergence weights and post-emergence growth. Juvenile Belding's ground squirrels raised by supplemented females emerged heavier than did juveniles raised by non-supplemented females, but did not grow more quickly after emergence (Trombulak 1991). In previous studies on Columbian ground squirrels (Dobson & Kjelgaard 1985a, 1985b), significant differences in emergence weights of supplemented and non-supplemented juveniles were detected only when data from all years and sites were pooled, suggesting that other sources of variation may be more important than supplementation effects. Limited variation in emergence weights of juveniles due to either supplementation or natural variation in food quality (Chapter 2) suggests that maternal influence explains little, if any, of the observed differences between HF and non-HF sites.

Food addition did affect post-weaning growth rates of juveniles; supplemented juveniles grew faster to maximum weight and through most of the two-week intervals. Growth to maximum weight of supplemented juveniles was similar to rates observed for juveniles on other sites with high quality food (Chapter 2), but the pattern of this growth differed. Growth rates of supplemented HF juveniles peaked in the first two weeks at levels similar to or higher than for juveniles on non-HF sites, and declined thereafter. Non-HF juveniles consumed high quality natural food (Chapter 2) and reached peak growth in the second two-week interval. Juveniles on non-HF sites may have grown faster in the second two weeks because food quality on those sites improved due to the effects of cattle grazing whereas supplemented HF juveniles had access to a supplement that was of constant quality and to plants that declined in quality partly because they were not grazed by cattle (Chapter 2).

Temporal changes in food quality may also explain differences between growth patterns of supplemented and non-supplemented HF juveniles, and growth patterns of juveniles studied in captivity by Koeppl and Hoffmann (1981). Those authors found a period of linear growth from 24 to 58 days after birth that was both preceded and followed by periods of slower growth. Juvenile S. columbianus emerge from natal burrows ≅28 days after birth (Murie & Harris 1982) so this period of linear growth encompasses the first four weeks after emergence; growth rates of both supplemented and non-supplemented HF juveniles declined during this period. Variation in food quality might explain these differences; HF juveniles obtained some (supplemented juveniles, pers. obs.) or all (non-supplemented juveniles) of their diet from plants that were declining in quality (Chapter 2) while juveniles studied under laboratory conditions received food that was constant in quality (Koeppl & Hoffmann 1981). Differences in timing of peak growth may be a function of inherently high phenotypic plasticity in this species (Dobson 1988) and a resultant ability to respond rapidly to changes in food quality. If this is the case, timing of growth may not be as important to juvenile survival as the total growth achieved.

In this study, high growth rates of juveniles were assumed to enhance survival because increased summer growth resulted in increased prehibernatory weights. Results from other supplemented Columbian ground squirrel populations support this assumption. Although growth rates were not determined, Dobson & Kjelgaard (1985a, 1985b) found that supplemented yearlings had higher spring emergence weights. With only minor variation in natal emergence weights, differences in spring emergence weights in that study were probably the result of differences in juvenile growth rates during the previous summer. Increased growth of supplemented HF juveniles probably results in higher prehibernatory weights that explains their increased survivorship relative to HF control juveniles.

Supplementation enhanced many life history traits of HF squirrels, often to levels seen in populations consuming high quality natural food (Chapter 2). The pattern and direction of changes in life history traits were generally the same as those observed in other populations of supplemented Columbian ground squirrels (Dobson & Kjelgaard 1985a, 1985b). This strongly suggests that differences in growth and survival between HF squirrels and squirrels in nearby colonies (Chapter 2) are due to differences in food quality, but alternative explanations should be considered.

Predation risk may be higher on HF than on other sites because HF is an open habitat that could aid commonly observed avian predators like the red-tailed hawk (Buteo jamaiciensis). HF juveniles may compensate for this risk by either changing their feeding rate or their level of vigilance. HF juveniles may reduce predation risk by feeding more rapidly than juveniles on other sites (Andrusiak & Harestad 1989, MacWhirter 1989) so they could acquire similar amounts of food even if they spent less time foraging. Juveniles might also ignore higher predation risk if maximizing growth had survival benefits that were greater than costs associated with decreased vigilance. MacWhirter (1989) found that time spent foraging increased over summer while vigilance declined; by extending their feeding bouts, HF juveniles could have total food intake similar to juveniles in other colonies. Given the potential for compensation and the importance of maximizing growth, it is unlikely that increased predation risk explains the differences in growth of juveniles observed between HF and other sites (Chapter 2).

Two other explanations for differences in squirrel growth and survival between HF and nearby sites have been suggested (J.F. Hare pers. comm.). One site, MB (Chapter 2), was artificially colonized (Wiggett & Boag 1986) and differences in growth between HF and MB juveniles could be the result of founder effects. The founders of MB were captured on HF, but they may not have been a random selection from that population raising the possibility that transplanted squirrels had inherently higher growth rates than the average for HF squirrels. Also, the potential for inherited differences in foraging ability exists (Ritchie 1991) so HF juveniles could be sub-optimal foragers compared to MB juveniles. However, a naturally colonized site (MC, Chapter 2), whose founders probably did not come from either MB or HF, has squirrels with life history traits that differ from HF squirrels in a manner similar to MB squirrels. This suggests a limited importance for founder effects.

Another possible alternative is higher levels of parasitism on HF causing reduced growth of juveniles. HF appears to have higher levels of biting flies (Athericidae) in July than either MC or MB (pers. obs.) and this could reduce foraging time. However, the flies are less active in the morning and evening when temperatures are cooler (pers. obs.) and squirrels tend to do most of their foraging (Betts 1976, Elliott & Flinders 1980). Additionally, populations of flies appeared to decline each year from 1994 to 1996 (pers. obs.), but ground squirrel growth rates differed between sites by similar amounts suggesting that attacks by flies were not affecting growth rates.

Although numbers of other ectoparasites (Hilton & Mahrt 1971a) were not quantified, occurrence of lice and fleas was noted when squirrels were captured. No large differences in numbers of ectoparasites were apparent between sites (pers. obs.). Endoparasites also occur in Columbian ground squirrels (Hilton & Mahrt 1971b, 1972) and their prevalence was unknown for my sites. However, there were no obvious reasons to believe parasitism rates differed significantly between colonies and, given their close proximity and occasional immigration between colonies, large differences in parasite communities or host susceptibility seem unlikely.

The pattern and magnitude of differences observed between HF squirrels and squirrels on non-HF sites appears to have changed over the past 20 years. HF has supported higher densities of squirrels in the past (Hare 1992) and survival rates were also higher in previous years (Boag & Murie 1981). These differences suggest that an important characteristic of HF may have changed, reducing the ability of HF squirrels to maximize growth. Forage quality can change due to grazing by cattle (Chapter 2) and grazing intensity by domestic livestock on HF is probably lower than it was in the past (J. O. Murie pers. comm.). Variation in forage quality seems to explain long term changes in life history traits of HF squirrels better than alternatives such as predation risk that vary yearly, but probably have not changed over the long term.

Results of this supplementation experiment suggest that food quality is a limiting factor for HF juveniles and this limitation leads to lower growth rates than for juveniles on other sites (Chapter 2). This experiment also provides some indication of the relative importance of protein and energy to growing juveniles. Whereas juvenile Columbian ground squirrels studied by Dobson & Kjelgaard (1985a, 1985b) were supplemented with food high in both energy and protein, HF juveniles had supplemental food (corn) with a digestible protein content lower than most of the natural food supply and digestible energy content higher than any mean value recorded for plants on HF and non-HF sites (Chapter 2). Similarity in response of squirrels in both studies suggests that energy, rather than protein, is limiting.

White (1978) suggested that protein was more important to growth and survival of juveniles than energy, but this conclusion was not supported by my supplementation experiment. However, confounding factors can make interpretation of these results more complex than is first apparent. Because corn is more digestible than the natural food supply (Chapter 2), turnover time for the digestive tract of juveniles may be reduced (Hume et al. 1993). Supplemented juveniles might then be able to fill their stomachs more often in a day than non-supplemented juveniles, which would enable them to have higher daily food consumption than non-supplemented juveniles. This could result in higher intake of all nutrients, including protein. Supplementation studies that account for confounding factors such as digestibility could potentially clarify the relationship between energy, protein and juvenile growth.

Literature Cited

Andrusiak, L.A. and Harestad, A.S. 1989. Feeding behavior and distance from burrows of Columbian ground squirrels. Can. J. Zool. 67:381-384.

Betts, B.J. 1976. Behavior in a population of Columbian ground squirrels, Spermophilus columbianus columbianus. Anim. Behav. 24:652-680.

Boag, D.A. and Murie, J.O. 1981. Population ecology of Columbian ground squirrels in southwestern Alberta. Can. J. Zool. 59:2230-2240.

Boutin, S. 1990. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Can. J. Zool. 68:203-220.

Choo, G.M., Waterman, P.G., McKey, D.B. and Gartlan, J.S. 1981. A simple enzyme assay for dry matter digestibility and its value in studying food selection by generalist herbivores. Oecologia 49:170-178.

Dobson, F.S. 1988. The limits of phenotypic plasticity in life histories of Columbian ground squirrels. In M.S. Boyce (ed.), Evolution of life histories of mammals. Yale University Press, New Haven, Conn. pp. 193-210.

Dobson, F.S., Badry, M.J. and Geddes, C. 1992. Seasonal activity and body mass of Columbian ground squirrels. Can. J. Zool. 70:1364-1368.

Dobson, F.S. and Kjelgaard, K.D. 1985a. The influence of food resources on population dynamics in Columbian ground squirrels. Can. J. Zool. 63:2095-2104.

_____. 1985b. The influence of food resources on life history in Columbian ground squirrels. Can. J. Zool. 63:2105-2109.

Elliott, C.L. and Flinders, J.T. 1980. Seasonal activity pattern of Columbian ground squirrels in the Idaho Primitive Area. Great Basin Nat. 40:175-177.

Festa-Bianchet, M. 1981. Reproduction in yearling female Columbian ground squirrels (Spermophilus columbianus). Can. J. Zool. 59:1032-1035.

Glazier, D.S. 1990. Reproductive efficiency and the timing of gestation and lactation in rodents. Am. Nat. 135:269-277.

Hare, J.F. 1992. Social discrimination by Spermophilus columbianus. Ph. D. thesis,University of Alberta, Edmonton.

Hilton, D.G.J. and Mahrt, J.L. 1971a. Ectoparasites from three species of Spermophilus (Rodentia: Sciuridae) in Alberta. Can. J. Zool. 49:1501-1504.

_____. 1971b. Eimeria spermophili n. sp. and other Eimeria spp. (Sporozoa: Eimeriidae) from three species of Spermophilus (Rodentia: Sciuridae) in Alberta. Can. J. Zool. 49:699-701.

_____. 1972. Taxonomy of trypanosomes (Protozoa: Trypanosomatidae) of Spermophilus spp. (Rodentia: Sciuridae). Parasitology 65:427-432.

Hume, I.D., Morgan, K.R. and Kenagy, G.J. 1993. Digesta retention and digestive performance in sciurid and microtine rodents: effects of hindgut morphology and body size. Physiol. Zool. 66:396-411.

King, W.J., Festa-Bianchet, M. and Hatfield, S. 1991. Determinants of reproductive success in female Columbian ground squirrels. Oecologia 86:528-534.

Koeppl, J.W. and Hoffmann, R.S. 1981. Comparative postnatal growth of four ground squirrel species. J.Mamm. 62:41-57.

Lima, S.L. and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68:619-640.

MacWhirter, R.B. 1989. Antipredator behaviour in the Columbian ground squirrel, Spermophilus columbianus: vigilance, alarm calling and escape responses. M.Sc. thesis, University of Alberta, Edmonton.

Murie, J.O. and Harris, M.A. 1982. Annual variation of spring emergence and breeding in Columbian ground squirrels (Spermophilus columbianus). J. Mamm. 63:431-439.

National Research Council. 1982. United States-Canadian tables of feed composition. 3rd revision. National Academy Press, Washington, D.C. pp.772.

Risch, T.S., Dobson, F.S. and Murie, J.O. 1995. Is mean litter size the most productive? A test in Columbian ground squirrels. Ecology 76:1643-1654.

Ritchie, M.E. 1991. Inheritance of optimal foraging behavior in Columbian ground squirrels. Evol. Ecol. 5:146-159.

Trombulak, S.C. 1991. Maternal influence on juvenile growth rates in Belding's ground squirrel (Spermophilus beldingi). Can. J. Zool. 69:2140-2145.

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

Wiggett, D.R. and Boag, D.A. 1986. Establishing colonies of squirrels during their active season. Wildl. Soc. Bull. 14:228-290.

Table 3.1. Survival rates of juvenile and adult ground squirrels. Juvenile survival rates were calculated by dividing the number of yearlings that emerged from hibernation in the spring by the total number of juveniles that emerged from natal burrows in the previous summer. Adult ground squirrel survival rates were determined by dividing the number of squirrels that emerged from hibernation by the number of squirrels present during the previous summer.

Winter period	Squirrel category	Non-supplemented		Supplemented[a]	
		North	Road	Station	Gorge
1995-96	Adult males	73% (11)[b]	85% (13)	88% (16)	80% (10)
1995-96	Adult females	94% (17)	71% (17)	84% (19)	90% (10)
1995-96	Juveniles[c]	17% (29)	16% (13)	91% (23)	56% (9)

[a] Supplemented with rolled corn ad lib. from May 27 to August 16 in 1995.

[b] Sample size

[c] Both sexes combined

Table 3.2. Mean weaning rates and mean litter sizes (±1S.E.) for 1995 and 1996. Weaning rates were calculated by dividing the number of females (yearlings excluded) that successfully raised juveniles to emergence by the number of females (yearlings excluded) still living on each site at the time of juvenile emergence. Mean litter sizes were calculated using only those females where proximity of the juveniles to the natal burrow or the female assured relatively high accuracy in determining litter size.

Year		Non-supplemented		Supplemented	
		North	Road	Station	Gorge
1995	Weaning rate	71% (17)[a]	47% (15)	92% (12)	33% (9)
1996	Weaning rate	47% (15)	45% (20)	90% (19)	60% (10)
1995	Litter size	2.7 ±0.3 (10)	2.0 ±0.2 (13)	2.2 ±0.2 (9)	2.3 ±0.3 (3)
1996	Litter size	2.4 ±0.3 (7)	2.3 ±0.2 (9)	2.9[b] ±0.1 (21)	2.7[c] ±0.3 (9)

[a] Sample size

[b] Excludes three yearlings that each weaned three juveniles.

[c] Excludes one yearling that weaned a litter of three juveniles.

Table 3.3. Emergence weights (g) and growth rates (g/day) of juvenile ground squirrels for 1995 and 1996 (±1S.E.). Only emergence weights for juveniles captured within 4 days after emergence from their natal burrow were included. Growth rates were calculated for four different weight periods. Growth to maximum weight is the maximum weight reached by the juvenile minus its emergence weight divided by the total number of days in this interval. The remaining three growth rate values represent growth rates in the six weeks after each ground squirrel emerges from its natal burrow divided into separate two week intervals.

Year	Weight period	Non-supplemented		Supplemented[a]	
		North	Road	Station	Gorge
1995	Emergence	**103.8** ±4.1 (8)[b]	**100.0** ±0.0 (2)	**103.8** ±3.8 (4)	**120** (1)
1996	Emergence	**103.3** ±12.0 (3)	**121.9** ±5.4 (8)	**118.3** ±3.4 (30)	**104.6** ±6.4 (12)
1995	Maximum weight[c]	4.3 ±0.3 (8)	n/a	6.7 ±0.3 (5)	n/a
1996	Maximum weight	4.5 ±0.5 (5)	4.3 ±0.2 (11)	5.9 ±0.2 (30)	6.1 ±0.3 (14)
1995	First two weeks	4.8 ±0.5 (11)	2.8 ±0.1 (2)	7.1 ±0.7 (7)	8.6 ±0.4 (5)
1996	First two weeks	7.3 ±1.8 (2)	5.0 ±0.6 (5)	6.7 ±0.6 (11)	10.1±0.4 (3)
1995	Second two weeks	5.3 ±0.4 (5)	1.8 ±0.2 (2)	6.6 ±0.4 (10)	8.5 (1)
1996	Second two weeks	3.9 (1)	2.5 ±0.6 (4)	5.5 ±0.7 (10)	6.7 ±0.6 (4)
1995	Third two weeks	3.1 ±0.4 (5)	n/a	7.1 ±0.4 (8)	7.9 (1)
1996	Third two weeks	n/a	5.8 (1)	5.2 ±0.5 (12)	5.9 ±0.6 (3)

[a] Supplemented with rolled corn ad lib. from May 27 to August 16.

[b] Sample size

[c] Only calculated for individuals recaptured and weighed at least 35 days after emergence from their natal burrow.

Figure 3.1. Mean rate of weight gain of non-supplemented (circles) and supplemented (squares) ground squirrels on HF from June 1 to August 15 in 1995 and 1996. Line ends indicate maximum and minimum group means for biweekly intervals within that period.

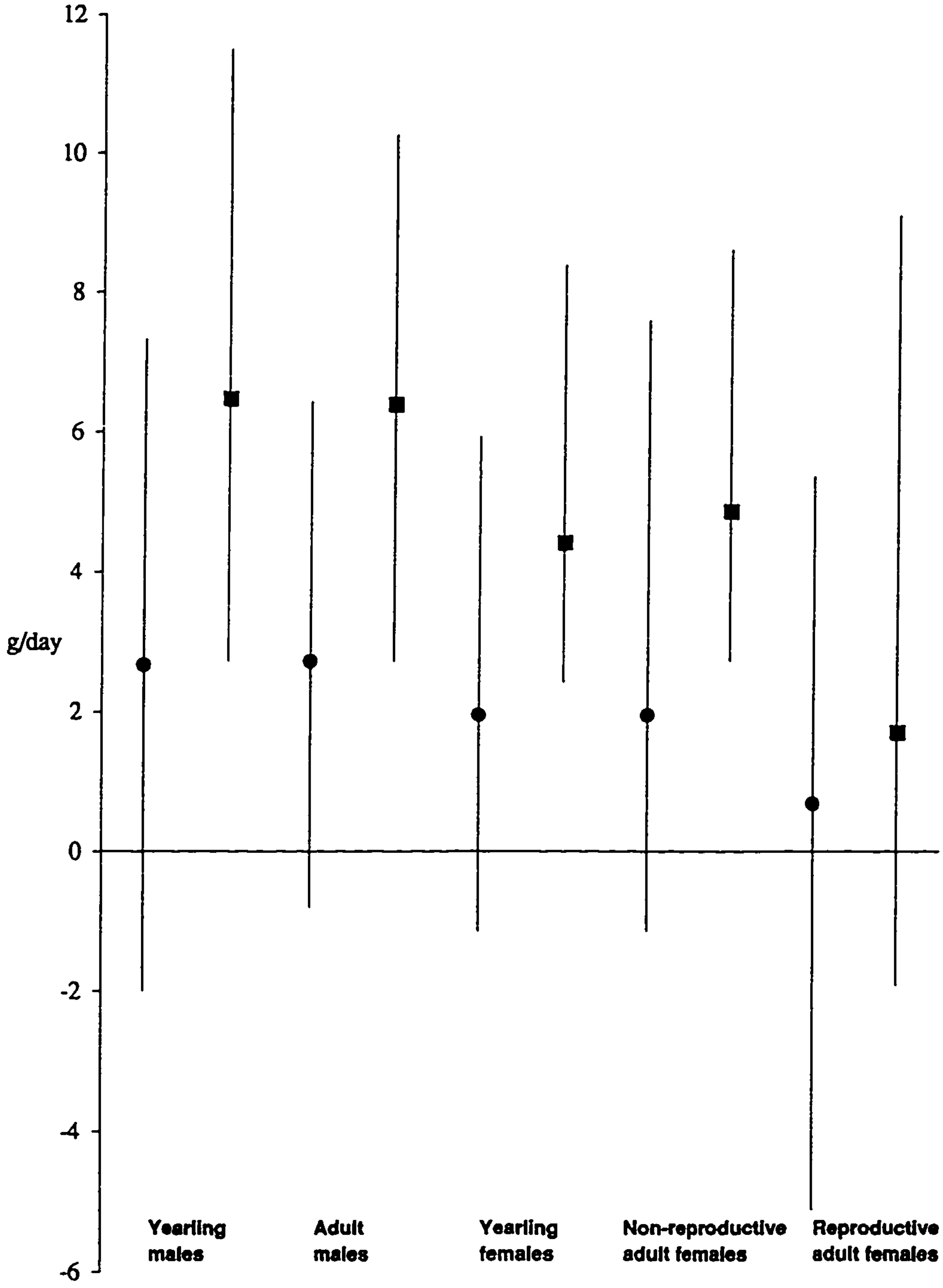
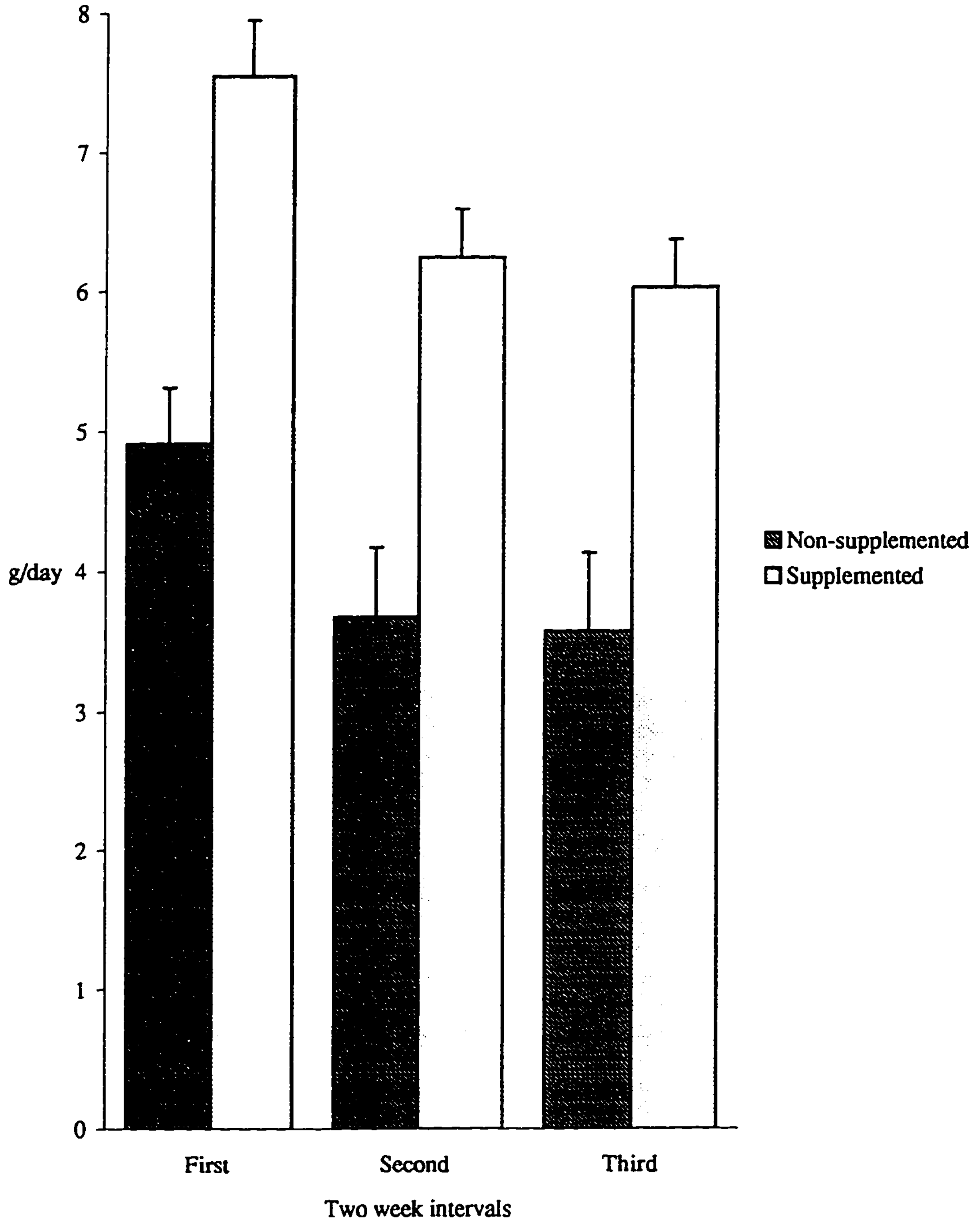


Figure 3.2. Mean growth rates (+1 S.E.) of non-supplemented and supplemented HF juveniles for successive two week intervals after emergence from natal burrows. Data pooled for both years (1995 and 1996) and sites (2 per treatment).



Chapter 4: Variation in Growth of Juvenile Columbian Ground Squirrels Consuming Diets With Differing Protein Content

Introduction

Growth and development of juveniles has been studied in many species of ground squirrels (Neal 1965, Clark 1970, Turner et al. 1976, Kiell & Millar 1978, Phillips 1981). In their comparative study, Koeppl and Hoffmann (1981) described growth curves of juveniles of four ground squirrel species including Columbian ground squirrels. These studies examined juveniles raised in a laboratory on a constant high quality diet, which provides a basis for interspecific comparisons and a standard when intraspecific variation is being studied, but does not explain why variation from this standard occurs.

Variation in growth rates of juvenile Columbian ground squirrels observed in wild populations may be due to differences in food quality (Dobson et al. 1992). Food quality differences probably lead to increased spring emergence weights of supplemented yearlings compared to non-supplemented yearlings (Dobson and Kjelgaard 1985a, 1985b) by increasing the growth rates of juveniles in the previous summer. Examining variation in food quality parameters such as energy and protein content in relation to juvenile growth may clarify the influence of these factors on growth rates.

Juveniles in Dobson and Kjelgaard's study (1985a, 1985b) consumed a supplement that was rich in both energy and protein. In another experiment (Chapter 3), supplemented juveniles in a ground squirrel colony (HF) grew ≅33% faster when only energy and not protein content was raised above that of natural foods. While those results suggest that energy may be a more limiting factor in juvenile growth than protein, this relationship needs to be reexamined to control for possible confounding variables in a free-ranging population.

Supplemented HF juveniles ate corn, a highly digestible food (75%, National Research Council 1982), but they also consumed plants that varied in digestibility (40.1 to 69.8%, Chapter 2), gross energy (3.96 to 4.14 kcal/g, Chapter 2) and crude protein content (8.4 to 16.9%, Chapter 2). Because corn was probably digested more rapidly than most plants, supplemented juveniles may have reduced turnover time of their digestive tracts (Hume et al. 1993) and increased total food consumption compared to non-supplemented juveniles. Thus, supplemented juveniles could potentially acquire more protein than non-supplemented juveniles producing increased growth through enhanced protein intake rather than increased energy intake.

This chapter presents the results of a laboratory experiment in which juveniles consumed rations that varied in protein content, but had similar energy content and digestibility. I assessed the relative importance of protein to juvenile growth when possible constraints of low energy content and digestibility were removed. I used these results in conjunction with data from juveniles consuming natural food of varying quality (Chapter 2) and juveniles supplemented in the wild (Chapter 3) to determine which factor, protein, energy or digestibility, is the more important food quality parameter influencing growth of juvenile Columbian ground squirrels.

Methods

This experiment was conducted in a laboratory building at the R.B. Miller Biological Station, 30 km west of Turner Valley, Alberta. The cage unit used consisted of 30 wire mesh cages (35 cm x 25 cm x 20 cm deep) mounted on a frame with 15 cages on either side, 3 cages high by 5 cages wide. Cages were suspended from the frame and waste material fell through the wire mesh floors onto collection trays. Each cage housed 1 juvenile and was supplied with a water bottle and a 15 cm long piece of 10 cm diameter black ABS plastic pipe to serve as a sleeping and hiding place.

Juvenile ground squirrels were obtained from two of the study sites, HF and MB, described in Chapter 2. Ten of the juveniles came from 3 MB females that were captured shortly before parturition and maintained in captivity until the juveniles were weaned (28 days old). The remaining juveniles came from HF where a total of 20 juveniles from 6 litters were captured shortly (<5 days) after emergence from their natal burrows. Each litter was tagged with individually numbered ear tags and placed in plexiglass cages in the laboratory for two days before the feeding trial commenced to allow for adjustment to captivity and weaning. During this adjustment period, the juveniles had free access to rodent chow, dog food, lettuce and water.

Juveniles within each litter were randomly assigned to experimental diets with at least one juvenile per litter assigned to each diet to control for litter effects. Because there were not sufficient juveniles available to start all individuals at the same time, the trials commenced on two different days. Ten juveniles (2 litters of 3 and 1 litter of 4) began their feeding trials on June 21 and the remaining 20 juveniles (4 litters of 3 and 2 litters of 4) started on July 2. At the end of the trial, HF juveniles were released near their original capture points and MB juveniles were released near main burrows on MB.

During the trial, juveniles were checked twice daily to ensure they had food and water, and preweighed amounts of food (25-50 g/day/juvenile) were provided each morning. If large amounts (>75 g) of food remained from the previous day, no additional food was provided. Food remaining in the food holder was weighed once each week when the juveniles were weighed. This value was subtracted from the total weight of food supplied during the week to provide estimates of food consumption. To assess food wastage, all material in the collecting trays under the cages (3 cages/day) was placed in a drying oven at 40° C for 24 h. The food in each of these dried samples was separated from fecal material and weighed. This process was repeated for each juvenile 3-4 times during the trial and the mean value of these samples was subtracted from estimates of food consumption for each juvenile to control for differences in food wastage.

Juveniles were weighed to the nearest 0.1g on an electronic scale when they began the feeding experiment and every 7 days thereafter for six weeks. Weighing was conducted before 10:00 A.M. and before additional food was placed in the cages to reduce weight variation due to differences in gut fill. After the weekly weighing, any juvenile that had not gained weight during the previous week was removed from the trial in accordance with animal care protocols.

During the feeding trial, juveniles received rations that had either low (8.5 %), medium (12.5 %) or high (16.5 %) levels of protein. These were standard test diets (5769C, 5771C and 5773C, respectively) supplied by PMI Feeds Inc. All protein in these diets came from casein and protein levels were increased or decreased at the expense of carbohydrate. All diets contained 3 % indigestible fibre. Crude protein and gross energy content of each ration (3 samples per ration) was assayed using the methods of Chapter 2 to verify the accuracy of stated diet specifications.

Growth rates (g/day) of juveniles were calculated by dividing the difference between weights at the beginning and end of the interval by the number of days between weighings. Feed efficiency values were calculated to determine whether the ability of juveniles to convert food into body mass varied due to dietary differences. To calculate feed efficiency (g food eaten/g weight gain), the total amount of food consumed in an interval was divided by the total weight gain during that interval. Both growth rates and feed efficiency values were calculated for each week and for the entire 6 week period of the trial.

Data analyses were similar to those used in Chapter 2. Effects of diets were compared using ANOVAs blocked by litter. In the 3 cases where there were two juveniles from a specific litter on the same diet, the mean of the values for both juveniles was used in the analyses.

Results

The test diets differed (F=1153.49, $p<0.001$) in crude protein content, and assayed values were similar to diet specifications (low=8.2 ±0.1%, medium=12.3 ±0.1%, high=16.6 ±0.2%). Gross energy content differed significantly (F=112.25, $p<0.001$) among diets. Tukey's tests indicated that the energy contents of the high protein diet (4.576 ±0.001 kcal/g) and medium protein diet (4.561 ±0.007 kcal/g) were similar, but greater than the energy content of the low protein diet (4.485 ±0.003 kcal/g).

Few differences between treatments were evident during the feeding trial. Rate of gain (Table 4.1) did not differ for either daily gain over the entire trial (F=0.52, p=0.61) or when weekly rates were compared using repeated measures ANOVA (F=1.39, p=0.29). Difference in weights at the beginning of the trial could have been a confounding variable, but mean weights then were not significantly different (F=2.21, p=0.15) between diets nor were they significant covariates in either the analysis of daily gain for the entire trial (F=0.49, p=0.50) or the analysis of weekly growth rates (F=2.05, p=0.18). Growth patterns (Figure 4.1) appeared to differ somewhat between treatments; as protein content increased, there was a trend towards higher peak growth rate with more rapid declines over the remainder of the trial. Juveniles eating the high protein diet had a higher peak gain and reached that peak earlier in the trial than either juveniles on the medium or low protein diets; juveniles on the medium protein diet had higher peak growth rates than the juveniles on low protein food, but peak growth occurred in the same week for both treatments.

Variation in feed efficiency (Table 4.2) followed patterns similar to those observed for weight gain. Higher protein content resulted in greater (i.e. smaller values) peak feed efficiency and earlier occurrence of these peaks. However, variation in protein content did not affect either total food consumption (F=0.26, p=0.78) or feed efficiency (entire trial: F=2.41, p=0.14, repeated measures ANOVA of weekly values: F=1.39, p=0.29).

More juveniles eating the high protein diet (3 juveniles) were removed from the trial than for the other diets (medium protein: 1 juvenile). These removals occurred on day 35 of the trial because these juveniles did not gain weight during the fifth week and, in some cases, they appeared to be entering torpor. Two juveniles, one from each of the medium and low protein diets, were removed from the trial in the first two weeks because they appeared to be ill. No data from these 2 juveniles were used in the analyses.

Discussion

Variation in protein content was expected to affect growth rates of juveniles because protein is often a limiting factor for juvenile growth (White 1978). Lack of variation in this trial suggests that either some food quality factors were limiting the growth of juveniles or they were growing close to the maximum rate determined by their genotype (Ricklefs 1968, 1973). The other main limiting factors, energy and digestibility, were similar among the test diets so the possibility of genetic limits to growth seems more plausible. This conclusion is supported by data from other portions of this study; growth rates during the first 35 to 45 days after emergence of both supplemented juveniles (5.9 to 6.7 g/day, Chapter 3) and juveniles consuming high quality natural food (6.0 to 6.5 g/day, Chapter 2) were similar to rates observed over the entire trial.

Case (1978) suggested that protein levels in excess of those found in their mother's milk would not substantially enhance growth rates of juveniles. Rodents have milk protein levels ranging from 6.3 to 11.2% (Robbins 1993) so it is possible that the low protein diet used in this trial provided sufficient protein to the juvenile ground squirrels. However, feeding trials with other rodents using casein based diets have found growth limitation and reduced feed efficiency of juveniles (rats:16.3% protein, mice:13.6% protein, Goettsch 1960), and weight loss in adults (hamsters:16.2% protein, DiBattista 1987), at protein levels higher than the upper values cited for milk protein. While my trial did not examine the relationship between growth limitation and the protein content of milk, it does suggest that juveniles are growing at maximum rates even at relatively low protein levels that may be similar to protein levels in their preweaning diet.

Although growth rates did not differ between treatments, growth patterns did vary slightly, which is useful for examining growth patterns of juveniles consuming other foods. Timing and magnitude of peak growth of juveniles consuming the low and medium protein diets were similar to juveniles eating high quality natural food (2.6 to 3.1 kcal/g digestible energy, 9.9 to 15.6% digestible protein, Chapter 2); in these cases, peak growth occurred in the third week after emergence. Peak growth of juveniles on the high protein diet was slightly higher than for juveniles supplemented with corn (3.1 kcal/g digestible energy, 6.0% digestible protein, Chapter 3) in a field study, but both groups exhibited peak growth in the second week after emergence. This suggests that both energy and protein content of the diet can limit growth rates and influence timing of peak growth, which is consistent with the concept of a first limiting nutrient where low levels of one nutrient can limit utilization of the other (Robbins 1993).

Variation in peak growth rates may also be a function of physiological setpoints for growth in relation to body condition (Robbins 1993). Juveniles must accumulate fat to survive hibernation (Murie & Boag 1984, Bachman 1994) and may have to switch from an emphasis on structural growth to a fattening phase to achieve sufficient fat reserves. Juveniles on the high protein diet reached peak growth in the second week, but declined thereafter possibly because they had reached a setpoint for structural growth where growth processes changed and fat accumulation was emphasized. This is supported somewhat by the higher number of juveniles on the high protein diet than for the other diets that appeared to enter torpor in the fifth week of the trial. The high protein diet juveniles may have started accumulating fat reserves earlier, and thus were ready for hibernation sooner than the other juveniles.

Variation in both magnitude and timing of peak growth may indicate an inherent ability of juvenile ground squirrels to maximize utilization of high quality food. Increases in feed efficiency that accompany increases in growth also support this conclusion. Columbian ground squirrels are a highly plastic species (Dobson 1988) that normally live in a highly variable natural environment (Chapter 2); the ability to maximize growth during periods of high food quality that are of unpredictable duration would be a valuable adaptation. However, while growth patterns differed, growth rates over the entire trial did not and this is probably more important to juveniles than growth patterns because total weight is an important determinant of juveniles' ability to survive hibernation (Murie & Boag 1984).

Crude protein content did not appear to limit growth rates at any of the levels used in this trial even though the protein content of both the low and medium diets was below levels shown to limit growth and feed efficiency of rats and mice (Goettsch 1960). Test diets with protein levels less than 8.5% should be utilized to determine the point at which protein content limits growth. However, some conclusions about the relative importance of crude protein, gross energy and digestibility can be made by comparing results from this trial with data from juveniles in natural populations and juveniles supplemented in the wild.

The crude protein content of the most common food, grasses, available to HF juveniles in the wild ranges from 8.4 to 13.6% which is within the range of variation of diets used in this trial. However, HF juveniles eating grass gained ≅2 g/day less (Chapter 2) than juveniles in this trial whereas HF juveniles fed a supplement (corn) with 8.0% crude protein content (Chapter 3) grew at rates similar to those recorded in this trial. This suggests that crude protein content alone is not a major component of diet quality for Columbian ground squirrels.

The use of gross energy as a food quality indicator was also assessed. Juveniles eating corn gained weight at rates similar to the juveniles in this trial, but because corn has ≅10% fewer kcal/g than the test diets, energy appeared not to be limiting in corn (4.13 kcal/g, Chapter 3). However, HF juveniles consuming a natural diet consisting mainly of grasses (≅4.12 kcal/g) grew more slowly (4.3 to 4.5 g/day) than supplemented HF juveniles despite the similarity of gross energy values. Large differences in growth rates of juveniles consuming diets with relatively similar energy values indicate that gross energy is not a good predictor of food quality.

The best predictor of food quality was digestibility. Growth rates of the trial juveniles (97% digestible diet), juveniles consuming high quality natural food (forbs: 64 to 75% digestibility, Chapter 2), and HF juveniles supplemented with corn (75% digestibility, National Research Council 1982) were similar to each other and all were higher than growth rates of non-supplemented HF juveniles which have a grass-dominated food supply (44 to 55% digestibility, Chapter 2). All of the juveniles in the faster growing groups had access to food that was more digestible than the diet of non-supplemented HF juveniles. The range of digestibility of the natural food supply on HF is lower than the critical range of 60 to 70% suggested for other ground squirrel species (Karasov 1982, Cork & Kenagy 1989). Lower digestibility may be a limiting factor for juveniles because it reduces their ability to utilize protein and energy contained in food (Robbins 1993), and it increases the turnover time of their digestive tract (Hume et al. 1993), which affects total daily food consumption. Research using diets varying in digestibility, but not protein or energy, would be useful to determine the level at which digestibility limits growth of juvenile ground squirrels. This could help to define the point at which each quality factor becomes the main factor influencing growth of juveniles and how interactions between these factors affect growth.

Literature Cited

Bachman, G.C. 1994. Food restriction effects on the body composition of free-living ground squirrels, Spermophilus beldingi. Physiol. Zool. 67:756-770.

Case, T.J. 1978. On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. Quar. Rev. Biol. 53:243-282.

Clark, T.W. 1970. Early growth, development and behavior of the Richardson ground squirrel (Spermophilus richardsoni elegans). Am. Midl. Nat. 83:197-205.

Cork, S.J. and Kenagy, G.J. 1989. Nutritional value of hypogeous fungus for a forest-dwelling ground squirrel. Ecology 70:577-586.

DiBattista, D. 1987. Control of protein intake in golden hamsters. Physiol. Behav. 39:1-10.

Dobson, F.S. 1988. The limits of phenotypic plasticity in life histories of Columbian ground squirrels. In M.S. Boyce (ed.), Evolution of life histories of mammals. Yale University Press, New Haven, Conn. pp. 193-210.

Dobson, F.S., Badry, M.J. and Geddes, C. 1992. Seasonal activity and body mass of Columbian ground squirrels. Can. J. Zool. 70:1364-1368.

Dobson, F.S. and Kjelgaard, K.D. 1985a. The influence of food resources on population dynamics in Columbian ground squirrels. Can. J. Zool. 63:2095-2104.

_____. 1985b. The influence of food resources on life history in Columbian ground squirrels. Can. J. Zool. 63:2105-2109.

Goettsch, M. 1960. Comparative protein requirements of the rat and mouse for growth, reproduction and lactation using casein diets. J. Nutr. 70:307-312.

Hume, I.D., Morgan, K.R. and Kenagy, G.J. 1993. Digesta retention and digestive performance in sciurid and microtine rodents: effects of hindgut morphology and body size. Physiol. Zool. 66:396-411.

Karasov, W.H. 1982. Energy assimilation, nitrogen requirements and diet in free-living antelope ground squirrels Ammospermophilus leucurus. Physiol. Zool. 55:378-392.

Kiell, D.J. and Millar, J.S. 1978. Growth of juvenile arctic ground squirrels (Spermophilus parryii) at McConnell River, N.W.T. Can. J. Zool. 56:1475-1478.

Koeppl, J.W. and Hoffmann, R.S. 1981. Comparative postnatal growth of four ground squirrel species. J.Mamm. 62:41-57.

Murie, J.O. and Boag, D.A. 1984. The relationship of body weight to overwinter survival in Columbian ground squirrels. J. Mamm. 65:688-690.

National Research Council. 1982. United States-Canadian tables of feed composition. 3rd revision. National Academy Press, Washington, D.C. pp.772.

Neal, B.J. 1965. Growth and development of the round-tailed and Harris antelope ground squirrels. Am. Midl. Nat. 73:479-489.

Phillips, J.A. 1981. Growth and its relationship to the initial annual cycle of the golden-mantled ground squirrel, Spermophilus lateralis. Can. J. Zool. 59:865-871.

Ricklefs, R.E. 1968. Patterns of growth in birds. Ibis 110:419-451.

_____.1973. Patterns of growth in birds. II. Growth rate and mode of development. Ibis 115:177-210.

Robbins, C.T. 1993. Wildlife feeding and nutrition. 2nd.ed. Academic Press Inc., San Diego. pp.352.

Turner, B.N., Iverson, S.L. and Severson, K.L. 1976. Postnatal growth and development of captive Franklin's ground squirrels (Spermophilus franklinii). Am. Midl. Nat. 95:93-102.

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

Table 4.1. Mean (±1 S.E.) growth rate (g/day) and initial weights (g) for juveniles fed rations with differing protein content. For juveniles born in the laboratory, the test began 2 days after they were weaned (≅30 days old). For juveniles captured after emergence in the field, the test began after a 2 day acclimatization period in the laboratory.

Test interval[a]	Protein content of test rations		
	8.5%	12.5%	16.5%
Initial weight	**151.7**	**133.5**	**143.1**
(Day 0)	±12.2	±6.4	±10.4
	(8)[b]	(8)	(9)
Weight gain	**5.9**	**6.9**	**6.6**
0-7 days	±0.7	±1.0	±0.5
	(8)	(8)	(9)
Weight gain	**7.1**	**8.1**	**9.8**
8-14 days	±1.1	±1.0	±0.8
	(8)	(8)	(9)
Weight gain	**7.6**	**8.2**	**6.0**
15-21 days	±0.8	±1.0	±0.9
	(8)	(8)	(9)
Weight gain	**6.5**	**6.2**	**5.5**
22-28 days	±0.6	±0.5	±0.8
	(8)	(8)	(9)
Weight gain	**5.5**	**3.7**	**2.1**
29-35 days	±0.9	±0.9	±1.0
	(8)	(8)	(9)
Weight gain	**3.0**	**3.4**	**2.6**
36-42 days	±0.9	±0.9	±0.8
	(8)	(7)	(6)
Weight gain	**5.9**	**6.2**	**6.2**
for entire test	±0.5	±0.5	±0.5
(0-42 days)	(8)	(7)	(6)

[a] The test started on Day 0 and ended on Day 42. Juveniles were weighed every 7 days during the test and daily growth rates for each week were calculated.

[b] Sample size

Table 4.2. Mean (±1 S.E.) feed efficiency (g food consumed/g weight gained) and total food consumption (g) for juveniles fed rations with differing protein content. For juveniles born in the laboratory, the test began 2 days after they were weaned (≅30 days old). For juveniles captured after emergence in the field, the test began after a 2 day acclimatization period in the laboratory. Feed efficiency values for juveniles that lost weight during a specific interval were not included because the resultant negative values for feed efficiency would artificially lower the mean value for that interval.

Test interval[a]	Protein content of test rations		
	8.5%	12.5%	16.5%
Total food consumption (0-42 days)	**1100.1** ±39.5 (8)[b]	**1062.1** ±62.6 (8)	**1094.5** ±42.9 (9)
Feed efficiency 0-7 days	**4.2** ±0.5 (8)	**3.8** ±0.8 (8)	**3.5** ±0.3 (9)
Feed efficiency 8-14 days	**4.3** ±0.9 (8)	**3.0** ±0.3 (8)	**2.8** ±0.2 (9)
Feed efficiency 15-21 days	**3.9** ±0.3 (8)	**3.9** ±0.4 (8)	**5.7** ±0.8 (9)
Feed efficiency 22-28 days	**4.6** ±0.3 (8)	**4.9** ±0.3 (8)	**5.4** ±0.6 (9)
Feed efficiency 29-35 days	**6.0** ±0.7 (8)	**9.6** ±3.9 (7)[c]	**10.0** ±3.5 (6)[d]
Feed efficiency 36-42 days	**12.4** ±1.1 (8)	**12.4** ±5.8 (7)	**7.8** ±1.7 (5)[e]
Feed efficiency for entire test (0-42 days)	**4.5** ±0.2 (8)	**4.1** ±0.2 (7)	**4.3** ±0.2 (6)

[a] The test started on Day 0 and ended on Day 42. Juveniles were weighed every 7 days during the test and daily growth rates for each week were calculated.

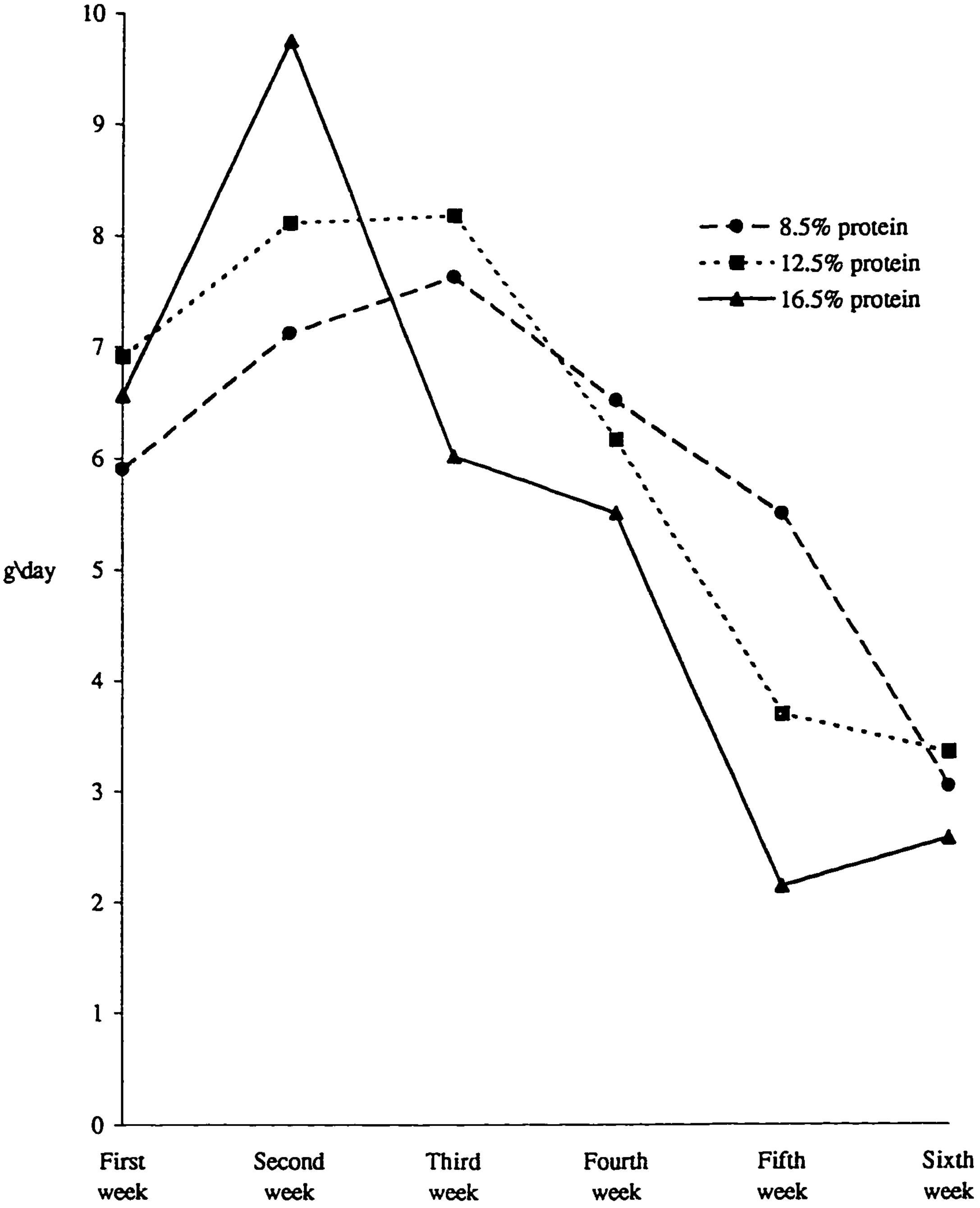
[b] Sample size

[c] Excludes one juvenile that lost weight during this interval.

[d] Excludes three juveniles that lost weight during this interval.

[e] Excludes one juvenile that lost weight during this interval

Figure 4.1. Mean daily growth rates of juvenile ground squirrels fed rations with differing protein content. Growth rates were calculated for 6 consecutive weeks after the feeding trial began. Refer to Table 4.1 for standard errors and sample sizes.



Chapter 5: Diet Selection of Reproductive Female Columbian Ground Squirrels

Introduction

Optimal foraging theory is based on the premise that natural selection will favour animals that maximize their intake of essential nutrients, which leads to optimal foraging patterns (Pyke, Pulliam & Charnov 1977). Optimal foraging usually requires diet selection, which has been documented in many rodents (Fagerstone et al. 1981, Belovsky 1986, Eshelman and Jenkins 1989, Frase & Armitage 1989). Among these diet selection studies, several pertain to Columbian ground squirrels (Lambeth & Hironaka 1982, Elliott & Flinders 1985, Harestad 1986, Andrusiak & Harestad 1989). Although plant communities differed among these studies, typically forbs were preferred to grasses. This pattern suggests that the nutritive content of these 2 plant groups differs (Belovsky 1986).

In his optimal foraging model for Columbian ground squirrels, Ritchie (1988) separated forage into forbs and grasses based on the higher digestible energy content of forbs. Forbs collected from ground squirrel colonies in southwestern Alberta had more digestible energy (25 to 40% more) and digestible protein (40 to 120% more) than did grasses (Chapter 2). The forb content of forage on these colonies varied and was related to squirrel growth and survival. For example, juveniles living on sites with more (17 to 35%) forbs had ≅50% faster growth and increased (≅ 500%) survivorship compared to juveniles living on sites with fewer (3 to 12%) forbs (Chapter 2). These patterns suggest that forbs are a nutritious food source that enhances ground squirrel fitness, and that squirrels should selectively forage for forbs.

In addition to nutritional differences, forbs and grasses also differ in the composition of their cuticular waxes, particularly the number of carbon atoms in the long chain alkanes (Dove & Mayes 1991). Because these alkanes are relatively resistant to digestion, they persist in fecal material and can serve as markers for food selection studies. By comparing levels of specific alkanes in feces to those in forbs and grasses, proportions of the diet represented by these 2 types of plants can be estimated (Mayes et al. 1986).

In this study, I used plant wax alkanes to estimate the forb content of the diet of reproductive adult females. Reproductive adult females were chosen because their reproductive success is influenced by variation in food quality (Dobson & Kjelgaard 1985a, 1985b, Chapter 2) and enhanced by optimal foraging (Ritchie 1990). I chose study sites with more (65 to 83%) grasses than forbs because females on these sites cannot rely on random encounter to gain the benefits of a forb-dominated diet (Ritchie 1990, Chapter 2), but must actively select forbs. I asked two questions: 1) do female Columbian ground squirrels select forbs over grasses? and 2) does diet selection differ after lactation ceases due to either changes in nutritional requirements (Glazier 1990, Robbins 1993) or increased availability of foraging areas resulting from reduced territoriality (Festa-Bianchet & Boag 1982)?

Methods

Fecal and plant samples were obtained from two ground squirrel colonies, MC and MB, during the summer of 1995. Plant samples were collected every 2 weeks from June 15 through July 30 as described in Chapter 2. Sample sizes were small (2-6/interval) because limited plant material remained after other chemical analyses (Chapter 2). Feces from reproductive adult (>1 year old) females were collected during regular trapping between May 31 and July 26 (Chapter 2); feces were dried for 48h at 40°C before storage.

Alkane content of the fecal samples and forb and grass portions of the forage samples were measured using the methods of Mayes et al. (1986). Samples were ground to fine powder and sub-samples (≅ 1 g forage, ≅ 0.4 g feces) were placed in 50 ml glass tubes. Internal standard (0.2 mg C_{34} dissolved in hexane), 10 ml methanol, and 1ml potassium hydroxide (45%) were added to each sample, and the tubes were sealed with Teflon lined caps and placed in a hot water bath (90 °C) for 4 h. After the tubes were removed from the water bath, 10 ml hexane and 5 ml water were added, the tubes were shaken for 1 minute, and left until the aqueous and hexane layers had separated. Hexane layers were removed by pipette and placed in clean test tubes. Water fractions were re-extracted with 8 ml of hexane and these hexane layers were added to the previous layers. Vials were placed on a hot plate and the hexane was evaporated under nitrogen gas to a volume of ≅ 0.5 ml. Reduced samples were poured onto individual columns that were made by placing a small amount of glass wool at the bottom of a 5 ml plastic pipette tip and then filling the tip ≅½ full with silica gel (60-200 mesh). Columns were eluted twice with 2.5 ml of hexane; plant pigments and wax lipids such as long-chain alcohols remained on the column while alkanes were recovered with the hexane. This hexane was stored in 20 ml glass vials until it was analyzed.

Alkane content of the extracted samples was measured using a Varian gas chromatograph with a flame ionization detector (290 °C) and fitted with an RTX-1 column (30 m x 0.25 mm with 0.25 um film). Column temperature increased from 90 °C to 270 °C @ 30 °C/minute with a 5 minute hold time; injector temperature increased from 100 °C to 290 ° C @ 150 °C/minute. Concentrations (mg/g of feces or forage) of 3 alkanes (C_{29} , C_{31} and C_{33}) were examined because they were expected to be most accurate in differentiating between forbs and grasses than shorter alkanes (Dove & Mayes 1991).

Alkane recovery rates from feces may vary with chain length (Dove & Mayes 1991) so correction factors were developed. Ten adult females from MB were held in plexiglass cages for 24 h and fed peanut butter containing equal quantities of alkane markers (C_{28} , C_{32} and C_{36}). Alkanes with even numbers of carbon atoms were used as markers because they occur at much lower concentrations in plants than do alkanes with odd number chains (Dove & Mayes 1991) so background levels do not affect measurements of recovery rates. Feces from these females were analyzed, recovery rates of the 3 markers were plotted against the carbon chain length, and the equation describing this relationship was used to extrapolate correction factors. Alkane (C_{29} , C_{31} and C_{33}) content values for each sample were divided by the appropriate factors to correct for differences in recovery rates.

Corrected values were used to determine the proportion of forbs and grasses in the feces by solving substitution equations of the following type:

$$af + bg = c \qquad \text{and} \qquad df + eg = h;$$

where c is the concentration of one alkane in the feces and h is the concentration of another alkane. The concentration of alkane c is a function of its concentration in forbs (a) and grasses (b), and the concentration of alkane h is a function of its concentration in forbs (d) and grasses (e). Equations were solved for f and g and individual values (f and g) were divided by their sum ($f + g$) to determine proportions of forbs and grasses in the diet.

The sampling period (May 31 to July 31) was divided into 4 equal intervals and the forb and grass content of fecal and plant samples were compared within these intervals. When 2 or more samples were available for a female within one interval, the mean of the samples was used. Forb content of feces and forage were also compared for the lactation and post-lactation period to determine if foraging patterns changed. Emergence dates of litters, used to establish lactation and post-lactation periods, were determined from trapping records (Chapter 2); results for fecal samples collected before or after a specific female's litter emerged were pooled for this analysis. Procedures for data analyses were described previously (Chapter 2). MB and MC data were analyzed separately using repeated measures ANOVAs.

Results

Linear regression was used to analyze recovery rates of marker alkanes fed to female ground squirrels. Recovery rates increased as alkane chain length increased ($F=16.68$, $p<0.001$, $r^2 = 0.37$). Correction factors ($C_{29} = 0.8762$, $C_{31} = 0.9101$ and $C_{33} = 0.9440$) were extrapolated from the regression equation, $y = 0.016972\,x + 0.38397$, where x is the number of carbons in a specific alkane. Results for 1 female were not used because low marker levels in the feces suggested the female had eaten little if any peanut butter.

Concentrations of 3 alkanes (C_{29} , C_{31} and C_{33}) in forbs and grasses (Appendix D.1) were compared to determine which 2 alkanes would be most sensitive for analyzing the forb and grass content of feces. The most useful pairs of alkanes are those that have similar total contents in forbs and grasses, but differ markedly in their ratios (Dove & Mayes 1991). As in other studies (reviewed by Dove & Mayes 1991), C_{29} and C_{33} appeared to be the most useful pair of alkanes for separating forbs and grasses. C_{31} is less useful because the concentration in forbs is intermediate between the other 2 alkanes so the ratios ($C_{31} : C_{29}$ and $C_{31} : C_{33}$) are more similar to those in grasses. The high concentration of C_{31} in grasses also reduces the sensitivity of this alkane because it increases the chances of swamping the contribution of forbs to the total fecal C_{31} concentration. Considering this, C_{29} and C_{33} were used to estimate forb content of feces.

Females selected forbs over grasses throughout the entire period of the study with the percentage in the feces ranging from 2 to 5 times greater than in the forage (Table 5.1); forb content of the forage and fecal samples differed for both MC ($F=316.24$, $p<0.001$) and MB ($F=61.56$, $p<0.001$). Dietary forb content did not change (MC: $F=0.81$, $p=0.39$, MB: $F=1.28$, $p=0.28$) after emergence of juveniles on either MC (lactation: 87.31 ±2.65%, n=9, post-lactation: 84.44 ±2.86%, n=9) or MB (lactation: 70.88 ±8.19%, n=13, post-lactation: 81.62 ±3.34%, n=13). Chromatographs of some fecal samples (MC: 3 samples, MB: 10 samples) were excluded from statistical analyses because the simultaneous equations gave unrealistic solutions of >100% forbs or grasses.

Discussion

Ground squirrels in this study showed a strong preference for forbs over grasses, which is consistent with results from most studies of foraging behavior in Columbian ground squirrels (Lambeth & Hironaka 1982, Harestad 1986, Andrusiak & Harestad 1989). In the only study that did not indicate a preference for forbs (Elliott & Flinders 1985), the ground squirrels lived on meadows with forb-dominated plant communities hence they could obtain the majority of their diet from forbs without actively selecting forbs. Based on optimal foraging theory (Pyke, Pulliam & Charnov 1977), this preference should enhance fitness and fitness benefits should be evident for females that select forbs.

MC and MB females have greater reproductive success (≅5 times greater) than do females living in nearby colonies with fewer forbs (>40% less, Chapter 2). Although this is strictly a correlative comparison, it is consistent with benefits of a forb-based diet indicated by Ritchie's optimal foraging model (1988). Optimal diets based on energy maximization usually contained more forbs than grasses (Ritchie 1988), and optimal foragers had greater litter sizes, growth rates and survivorship compared to non-optimal foragers (Ritchie 1990). Additionally, females consuming diets that deviated from the optimum in favour of forbs experienced smaller declines in reproductive success than those whose diets deviated in favour of grasses (Ritchie 1991). This suggests that the strong preference for forbs exhibited by MC and MB females serves to enhance their reproductive success.

Although the higher digestible energy and protein content of MC and MB forbs compared to grasses (Chapter 2) suggests that ground squirrels should always select forbs, selection could be influenced by other quality factors. Ritchie (1988) suggested that high water content of forbs is a constraint that reduces time necessary to fill the gut, but also reduces nutrient concentration; this leads, in some cases, to selection of grasses. However, no allowance was made for differences in passage rates between grasses and forbs; grasses contain more fibre than forbs (Chapter 2) and fibre content is probably more constraining than water content because gut retention times are higher for particles than for fluids (Hume et al. 1993). Rather than a balance between plant quality factors, the ratio of forbs to grasses in the diet is more likely determined by a preference for forbs that is limited by their relative availability (i.e. encounter rate).

Factors other than plant quality may influence forage selectivity. Increases in territory quality (i.e. enhanced food quality) lead to increased territorial defence that can affect foraging patterns of adjacent squirrels (Boag & Wiggett 1994). Territoriality declines after juvenile emergence (Festa-Bianchet & Boag 1982) allowing females to forage in areas that were unavailable to them during lactation so, if these areas differ in forb content, lactation and post-lactation diets could differ. Differences in nutritional demands after lactation ceases (Glazier 1990, Robbins 1993) could also lead to changes in the composition of an optimal diet. However, there was no evidence that MC and MB females altered their foraging preferences after lactation which suggests that territorial behavior does not have a major effect on foraging patterns of these females, and that any changes in nutritional requirements after lactation do not affect food selection.

Results from this study should be viewed with caution because some samples produced unrealistic results (i.e. >100% forbs or grasses). Because the majority (10 of 13) of these samples indicated >100% forbs in the feces, it is possible that the ratios of alkanes in the plant samples were skewed in favour of forbs leading to overestimation of the forb content of all the feces. However, differences in forb content between the feces and plant samples were large and were unlikely to be solely the result of analytical error. Results for MC are probably more reliable because most (10 of 13) of the unrealistic results came from MB samples.

These analytical problems were probably due to insufficient sampling of plants so the means for alkane content of forbs and grasses did not accurately reflect the alkane content of plants consumed by the ground squirrels. Alkane content can change as plants mature (Dove & Mayes 1991) and this could have affected the results. Grazing can delay plant maturation (Burton et al. 1964, Goldberg et al. 1980); plants used to estimate alkane content of the forage had been protected from grazing for 2 weeks prior to collecting, whereas the squirrels were consuming forage that was constantly exposed to grazing (Chapter 2). This could explain why MB, which has a plant community that is more variable in both composition and stage of maturity than MC (pers. obs), had more samples with unrealistic solutions.

It is also possible that differences in dispersion of plants within sites could affect forb availability within females' territories. This could lead to inaccurate estimation of the degree of selection for forbs because within-site variation in plant distribution was not accounted for in this study. A more rigorous sampling regime involving plant sampling at the same time as feces collection and at sites where females were observed foraging, increased numbers of samples, and assessment of differences in plant communities between territories would improve accuracy in evaluating diet selection.

Literature Cited

Andrusiak, L.A. and Harestad, A.S. 1989. Feeding behavior and distance from burrows of Columbian ground squirrels. Can. J. Zool. 67:381-384.

Belovsky, G.E. 1986. Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. Oecologia 70:35-52.

Boag, D.A. and Wiggett, D.R. 1994. Food and space: resources defended by territorial parous female Columbian ground squirrels. Can. J. Zool. 72:1908-1914.

Burton, G.W., Knox, F.E. and Beardsley, D.W. 1964. Effect of age on the chemical composition, palatability and digestibility of grass leaves. Agron. J. 56:160-162.

Dobson, F.S. and Kjelgaard, K.D. 1985a. The influence of food resources on population dynamics in Columbian ground squirrels . Can. J. Zool. 63:2095-2104.

_____. 1985b. The influence of food resources on life history in Columbian ground squirrels. Can. J. Zool. 63:2105-2109.

Dove, H. and Mayes, R.W. 1991. The use of plant wax alkanes as marker substances in studies of the nutrition of herbivores: a review. Aust. J. Agric. Res. 42:913-952.

Elliott, C.L. and Flinders, J.T. 1985. Food habits of the Columbian ground squirrel, Spermophilus columbianus, in southcentral Idaho. Can. Field Nat. 99:327-330.

Eshelman, B.D. and Jenkins, S.H. 1989. Food selection by Belding's ground squirrels in relation to plant nutritional features. J. Mamm. 70:846-852.

Fagerstone, K.A., Tietjen, H.P. and Williams, O. 1981. Seasonal variation in the diet of black-tailed prairie dogs. J. Mamm. 62:820-824.

Festa-Bianchet, M. and Boag, D.A. 1982. Territoriality in adult female Columbian ground squirrels. Can. J. Zool. 60:161-172.

Frase, B.A. and Armitage, K.B. 1989. Yellow-bellied marmots are generalist foragers. Ethol. Ecol. Evol. 1:353-366.

Glazier, D.S. 1990. Reproductive efficiency and the timing of gestation and lactation in rodents. Am. Nat. 135:269-277.

Goldberg, M., Tabroff, N.R. and Tamarin, R.H. 1980. Nutrient variation in beach grass in relation to beach vole feeding. Ecology 61:1029-1033.

Harestad, A.S. 1986. Food habits of Columbian ground squirrels: a comparison of stomach and fecal samples. The Murrelet 67:75-78.

Hume, I.D., Morgan, K.R. and Kenagy, G.J. 1993. Digesta retention and digestive performance in sciurid and microtine rodents: effects of hindgut morphology and body size. Physiol. Zool. 66:396-411.

Lambeth, R. and Hironaka, M. 1982. Columbian ground squirrels in subalpine forest openings in central Idaho. J. Range Manage. 35:493-497.

Mayes, R.W., Lamb, C.S. and Colgrove, P.M. 1986. The use of dosed and herbage n-alkanes as markers for the determination of herbage intake. J.Agric. Sci. 107:161-170.

Pyke, G.H., Pulliam, H.R. and Charnov, E.L. 1977. Optimal foraging: a selective review of theory and tests. Quar. Rev. Biol. 52:137-154.

Ritchie, M.E. 1988. Individual variation in the ability of Columbian ground squirrels to select an optimal diet. Evol. Ecol. 5:232-252.

_____. 1990. Optimal foraging and fitness in Columbian ground squirrels. Oecologia 82:71-86.

_____. 1991. Inheritance of optimal foraging behavior in Columbian ground squirrels. Evol. Ecol. 5:146 -159.

Robbins, C.T. 1993. Wildlife feeding and nutrition. 2nd.ed. Academic Press Inc., San Diego. pp.352.

Table 5.1. Mean forb content (%) of plant material and feces collected from MC and MB in 1995. Forb content was determined by comparing the amounts of plant wax alkanes (C_{29} and C_{33}) present in the feces to the amounts in forbs and grasses using simultaneous substitution equations. Some solutions for these equations gave unrealistic answers (i.e. >100% forb or grass) and were excluded from the analyses (see footnotes).

Time interval	MC		MB	
	Plant material	Feces	Plant material	Feces
May 31-June 15	**23.2** ±2.6 (20)[a]	**88.0** ±4.0 (9)[b]	**35.0** ±5.0 (20)	**67.4** ±9.0 (12)[c]
June 16-June 30	**29.5** ±2.4 (20)	**80.8** ±2.9 (9)	**26.3** ±2.7 (20)	**88.2** ±1.2 (15)
July 1-July 15	**16.6** ±2.6 (13)	**88.5** ±3.6 (8)[d]	**28.2** ±3.9 (20)	**77.2** ±5.6 (9)[e]
July 16-July 31	**25.8** ±3.0 (16)	**83.3** ±3.8 (7)[f]	**20.7** ±3.8 (19)	**76.8** ±9.2 (8)[g]

[a] Sample size

[b] Excludes 1 sample

[c] Excludes 2 samples

[d] Excludes 1 sample

[e] Excludes 4 samples

[f] Excludes 1 sample

[g] Excludes 4 samples

Chapter 6: Concluding Discussion

High quality food, both natural (Chapter 2) and supplemental (Chapter 3), increases growth rates and overwinter survivorship of juveniles, and enhances the reproductive success of their dams (King et al. 1991). Correlative comparisons suggest that high forb content in forage is indicative of high quality food because forbs contain more protein and are more digestible than are grasses (Chapter 2). However, experimental manipulation of protein content did not cause growth rates of juveniles to vary (Chapter 4); all rates were similar to those of juveniles on high forb sites even for protein levels at the lower end of the range of natural variation (Chapter 2). This suggests that protein does not limit growth of HF juveniles.

Supplementation with highly digestible, energy-rich food (i.e. corn) increased growth rates of HF juveniles to levels observed on sites with high forb content (Chapter 2 & 3), suggesting that increased energy can enhance growth. However, energy content does not differ between forbs and grasses and there is little seasonal variation in energy content within these groups (Chapter 2). The common component among all high quality foods (Chapter 2: forbs, Chapter 3: rolled corn, Chapter 4: test rations) was high digestibility. Digestibility appears to be the primary limiting factor (Robbins 1993) in the diet of juveniles probably because they are constrained by their digestive capacity (Hume et al. 1993). Although low digestibility of food has limited effects on female reproductive success via reduction in litter sizes and weaning rates, it reduces reproductive success (King et al. 1991) by limiting growth and reducing survivorship of juveniles (Chapter 2 & 3). Experimental variation of digestibility could provide further evidence of how digestibility influences growth, survival and reproductive success.

Examination of diet selection in adult females (Chapter 5) indicated a strong preference for high quality food, namely forbs, which could enhance reproductive success in two ways. Consuming forbs could have direct benefits by increasing spring emergence weights of females and positively influencing litter sizes and weaning rates (King et al. 1991, Risch et al. 1995). Selection of forbs by females could also have indirect benefits because juveniles acquire foraging behaviors (i.e. optimal or sub-optimal) from their mothers (Ritchie 1991), which could influence juvenile growth and survival. Studying diet selection in juveniles could indicate whether they can adequately identify high quality food or, as Ritchie (1991) suggests, whether they are more likely to be sub-optimal foragers than adults. This could show how (i.e. directly or indirectly) optimal foraging enhances female reproductive success.

Lower growth rates of HF juveniles compared to MC and MB juveniles are at least partially due to lower availability of forbs (Chapter 2). The absence of cattle grazing on HF may explain the paucity of forbs relative to MC and MB (Chapter 2), but the absence of replicates for HF limits interpretation; adding one or more ungrazed sites to this study would allow broader application of the results. Despite this limitation, my study clarifies the relationship between food quality variation and growth of juvenile ground squirrels.

Food quality differences have frequently been used to explain life history variation in Columbian ground squirrels (Festa-Bianchet 1981, Lambeth & Hironaka 1982, Dobson & Kjelgaard 1985, Dobson & Murie 1987, Ritchie 1990, Boag & Wiggett 1994). This study shows that high food quality can enhance growth and survival of juveniles, which increases female reproductive success (King et al. 1991). Food quality, both within and between ground squirrel colonies, can be measured in gross terms by assessing forb content of the forage and, at a finer scale, by estimating digestibility of the forage.

Literature Cited

Boag, D.A. and Wiggett, D.R. 1994. Food and space: resources defended by territorial parous female Columbian ground squirrels. Can. J. Zool. 72:1908-1914.

Dobson, F.S. and Kjelgaard, K.D. 1985. The influence of food resources on life history in Columbian ground squirrels. Can. J. Zool. 63:2105-2109.

Dobson, F.S. and Murie, J.O. 1987. Interpretation of intraspecific life history patterns: evidence from Columbian ground squirrels. Am. Nat. 129:382-397.

Festa-Bianchet, M. 1981. Reproduction in yearling female Columbian ground squirrels (*Spermophilus columbianus*). Can. J. Zool. 59:1032-1035.

Hume, I.D., Morgan, K.R. and Kenagy, G.J. 1993. Digesta retention and digestive performance in sciurid

King, W.J., Festa-Bianchet, M. and Hatfield, S. 1991. Determinants of reproductive success in female Columbian ground squirrels. Oecologia 86:528-534.

Lambeth, R. and Hironaka, M. 1982. Columbian ground squirrels in subalpine forest openings in central Idaho. J. Range Manage. 35:493-497.

Risch, T.S., Dobson, F.S. and Murie, J.O. 1995. Is mean litter size the most productive? A test in Columbian ground squirrels. Ecology 76:1643-1654.

Ritchie, M.E. 1990. Optimal foraging and fitness in Columbian ground squirrels. Oecologia 82:71-86.

_____. 1991. Inheritance of optimal foraging behavior in Columbian ground squirrels. Evol. Ecol. 5:146 -159.

Robbins, C.T. 1993. Wildlife feeding and nutrition. 2nd.ed. Academic Press Inc., San Diego. pp.352.

Appendix A.1. Comparison of overwinter survival rates, revised survival rates, and recapture rates of juveniles for preliminary study season and rationale for calculations used in the entire study.

Winter Period	Trapping Grid	Overwinter Survival Rate[a]	Revised Survival Rate[b]	Percentage of Surviving Juveniles Not Recaptured[c]
1994-95	MC	71%	90%	9%
		(34)	(21)	(34)
1994-95	MB	77%	87%	16%
		(43)	(30)	(43)
1994-95	HF	15%	20%	8%
		(13)	(5)	(13)

[a] # of juveniles surviving hibernation divided by # of juveniles that emerged from natal burrows the previous summer.

[b] # of juveniles surviving hibernation divided by # of juveniles recaptured ≥35 days after emergence from natal burrows the previous summer.

[c] # of juveniles surviving hibernation that were not recaptured ≥35 days after emergence from natal burrows divided by # of juveniles that emerged from natal burrows the previous summer.

Rationale

Calculations of overwinter survival rates as used in Chapter 2 measure loss from all sources including summer losses due to predation. This is probably not a major concern with adult squirrels because total mortality is generally lower than for juveniles (Table 1) and recaptures are more consistent (pers. obs.), but it may present a problem with juvenile squirrels. Limiting the number of animals to only those juveniles recaptured later in summer (Revised survival rate) reduces the number of non-hibernation deaths included in overwinter survival rates. The relative magnitude and direction of differences are unchanged for the revised rates. Sample size is reduced because some juveniles are difficult to recapture during summer (last column) and do not appear in calculations of revised rates. If surviving and non-surviving juveniles had similar recapture rates, then the time of disappearance of up to 16% of juveniles could not be assessed.

Revised survival rates could also be biased due to the trapping pattern used to recapture juveniles. Because gathering data on growth rates was the priority for trapping, trapping after juveniles emerged was concentrated in areas where juveniles were captured the previous week. As a result, sites (particularly HF) were not trapped uniformly during this period so chance of recapture was smaller for juveniles that moved away from the area near their natal burrow and for juveniles living on peripheral areas of grids. Assuming these individuals experienced summer death loss (as in the revised survival rate) would be erroneous. Trapping in the spring was more uniform, but potential problems occurred on HF grids where juveniles may have moved off grids into adjacent areas before hibernation and were outside the area trapped the following spring. Although overwinter survival rates used in this study may overestimate losses during hibernation they are reflective of differences between sites, provide larger sample sizes, and are not biased by differences in recapture rates.

Appendix A.2. Mean rate of weight change (g/day) for adult (>1 year old) males during successive two week intervals in 1995 and 1996 (±1 S.E.). To calculate these values, the weight closest (±3 days) to the beginning of a specific interval was subtracted from the weight closest (±3 days) to the end of the interval for the same animal and the difference between these two weights was divided by the number of days between them.

Time period	MC		MB		HF	
	1995	1996	1995	1996	1995	1996
May1-15	**-2.0** ±0.8 (5)[a]	**-6.1** ±1.1 (4)	**-2.2** ±0.9 (11)	**-4.0** ±1.2 (8)	**0.7** ±0.9 (6)	**-2.8** ±0.8 (7)
May16-31	**4.9** ±0.5 (6)	**5.8** ±1.6 (3)	**5.1** ±0.5 (11)	**5.5** ±0.7 (8)	**2.3** ±0.8 (9)	**1.7** ±0.7 (11)
June1-15	**2.0** ±0.4 (4)	**2.7** ±0.5 (4)	**4.9** ±0.8 (9)	**5.2** ±0.6 (11)	**3.0** ±0.5 (10)	**2.9** ±0.4 (9)
June16-30	**6.8** ±0.5 (4)	**7.9** ±2.2 (3)	**4.1** ±0.7 (9)	**7.0** ±1.7 (5)	**2.1** ±0.5 (10)	**1.7** ±0.8 (7)
July1-15	**6.7** ±0.8 (6)	**5.7** ±3.6 (2)	**8.7** ±1.1 (7)	**7.1** ±0.9 (5)	**3.4** ±0.5 (5)	**6.8** ±0.3 (2)
July16-31	**4.3** ±0.7 (6)	**5.5** ±2.4 (3)	**1.7** ±1.0 (7)	**1.7** ±0.8 (7)	**-0.8** ±2.0 (2)	**5.4** ±0.6 (3)
August 1-15	**2.9** ±0.7 (2)	n/a	n/a	n/a	n/a	**1.5** ±2.0 (3)

[a] Sample size

Appendix A.3. Mean rate of weight change (g/day) for yearling males during successive two week intervals in 1995 and 1996 (±1 S.E.). To calculate these values, the weight closest (±3 days) to the beginning of a specific interval was subtracted from the weight closest (±3 days) to the end of the interval for the same animal and the difference between these two weights was divided by the number of days between them.

Time period	MC		MB		HF	
	1995	1996	1995	1996	1995	1996
May1-15	**3.1** ±0.2 (2)[a]	**-6.2** ±1.0 (4)	**3.4** ±0.2 (14)	**-2.4** ±0.9 (7)	n/a	n/a
May16-31	**5.8** ±0.5 (6)	**8.8** ±1.0 (3)	**6.3** ±0.2 (17)	**7.2** ±0.8 (8)	**4.1** ±1.3 (3)	n/a
June1-15	**2.0** ±0.5 (6)	**3.3** ±0.8 (3)	**2.5** ±0.3 (15)	**4.6** ±0.2 (10)	**3.8** ±0.4 (5)	**5.4** (1)
June16-30	**3.9** ±0.4 (2)	**4.8** ±2.8 (3)	**2.4** ±0.4 (14)	**2.4** ±0.9 (2)	**1.9** ±0.7 (5)	**4.0** (1)
July1-15	**5.2** ±1.3 (2)	n/a	**4.7** ±1.5 (4)	**4.6** (1)	**2.7** ±4.7 (2)	n/a
July16-31	**7.6** ±0.7 (3)	n/a	**3.5** ±1.1 (4)	n/a	**1.7** ±1.0 (2)	n/a
August 1-15	**4.3** (1)	n/a	**-2.1** ±0.4 (3)	n/a	**2.7** (1)	**-1.4** (1)

[a] Sample size

Appendix A.4. Mean rate of weight change (g/day) for yearling females during successive two week intervals in 1995 and 1996 (±1 S.E.). To calculate these values, the weight closest (±3 days) to the beginning of a specific interval was subtracted from the weight closest (±3 days) to the end of the interval for the same animal and the difference between these two weights was divided by the number of days between them.

Time period	MC		MB		HF	
	1995	1996	1995	1996	1995	1996
May1-15	**2.2**	n/a	**2.9**	**-0.9**	**4.6**	n/a
			±0.4	±0.7		
	(1)[a]		(8)	(3)	(1)	
May16-31	**4.9**	**3.1**	**5.5**	**5.3**	**4.9**	**4.2**
	±0.5	±0.4	±0.4	±0.6	±1.1	±0.8
	(6)	(3)	(14)	(8)	(3)	(2)
June1-15	**0.2**	**2.5**	**1.5**	**3.8**	**1.1**	**4.0**
	±1.4	±0.4	±0.4	±0.5	±2.2	±0.4
	(5)	(3)	(12)	(8)	(2)	(5)
June16-30	**2.7**	**1.1**	**2.1**	**3.9**	**1.0**	**3.3**
	±0.8		±0.3	±0.3	±0.3	±0.4
	(3)	(1)	(11)	(6)	(5)	(4)
July1-15	**3.1**	**2.9**	**6.0**	**3.8**	**2.7**	**2.5**
	±1.1	±1.8	±0.7	±0.2	±0.5	±0.3
	(4)	(2)	(7)	(4)	(2)	(2)
July16-31	**4.7**	**4.3**	**1.9**	**1.1**	**0.4**	**2.9**
	±0.8	±1.4	±0.3	±0.5	±1.3	±1.7
	(6)	(2)	(10)	(5)	(3)	(2)
August 1-15	**1.0**	n/a	n/a	n/a	**-0.2**	**3.2**
	±1.0				±0.2	±1.5
	(3)				(4)	(2)

[a] Sample size

Appendix A.5. Mean rate of weight change (g/day) for successive two week intervals in 1995 and 1996 for adult (>1 year old) non-reproductive females (±1 S.E.). To calculate these values, the weight closest (±3 days) to the beginning of a specific interval was subtracted from the weight closest (±3 days) to the end of the interval for the same animal and the difference between these two weights was divided by the number of days between them.

Time period	MC		MB		HF	
	1995	1996	1995	1996	1995	1996
May1-15	**6.0**	**-3.1**	**3.3**	**-1.6**	**4.5**	**0.0**
	±2.7	±0.9	±0.6	±0.3	±0.1	±0.5
	(3)[a]	(9)	(7)	(14)	(2)	(5)
May16-31	**2.4**	**6.3**	**2.2**	**5.8**	**3.8**	**4.8**
	±1.1	±0.5	±0.7	±0.5	±1.3	±0.7
	(5)	(7)	(7)	(13)	(6)	(13)
June1-15	**-0.1**	**2.2**	**2.3**	**2.5**	**1.3**	**4.1**
	±1.1	±0.5	±0.5	±0.2	±0.5	±2.0
	(3)	(8)	(6)	(15)	(9)	(16)
June16-30	**3.4**	**3.4**	**1.4**	**4.0**	**0.3**	**1.3**
	±0.2	±0.6	±1.1	±0.6	±0.6	±0.7
	(2)	(5)	(5)	(12)	(12)	(12)
July1-15	**5.8**	**4.9**	**5.2**	**5.5**	**2.5**	**3.6**
	±0.4	±1.0	±0.8	±0.4	±1.2	±0.5
	(3)	(8)	(6)	(9)	(5)	(8)
July16-31	**3.6**	**4.4**	**1.3**	**0.3**	**1.4**	**3.1**
		±1.0	±0.7	±0.7	±1.0	±1.4
	(1)	(6)	(6)	(3)	(5)	(6)
August 1-15	n\a	n\a	n\a	n\a	**0.2**	**-0.3**
					±0.4	±1.5
					(7)	(4)

[a] Sample size

Appendix A.6. Mean rate of weight change (g/day) for successive two week intervals in 1995 and 1996 for adult (>1 year old) reproductive females (±1 S.E.). To calculate these values, the weight closest (±3 days) to the beginning of a specific interval was subtracted from the weight closest (±3 days) to the end of the interval for the same animal and the difference between these two weights was divided by the number of days between them.

Time period	MC		MB		HF	
	1995	1996	1995	1996	1995	1996
May1-15	1.9 ±0.3 (3)[a]	-1.4 ±0.5 (5)	3.9 ±0.4 (12)	-1.5 ±0.4 (9)	n/a	-0.4 ±0.2 (2)
May16-31	1.4 ±1.0 (8)	1.9 ±0.7 (6)	1.0 ±0.8 (15)	4.2 ±1.5 (6)	2.1 ±2.0 (4)	5.6 ±1.0 (9)
June1-15	-0.3 ±1.2 (9)	0.7 ±0.4 (7)	-1.2 ±0.4 (15)	0.6 ±0.7 (5)	-0.9 ±1.1 (6)	0.8 ±0.6 (9)
June16-30	-0.6 ±0.6 (9)	0.7 ±1.0 (7)	-3.2 ±0.9 (15)	2.6 ±1.6 (4)	-4.3 0.7 (7)	-0.2 ±0.5 (8)
July1-15	2.5 ±0.6 (8)	5.5 ±1.1 (7)	6.2 ±1.2 (9)	5.6 ±0.8 (4)	3.0 ±0.7 (8)	0.0 ±0.7 (7)
July16-31	6.1 ±0.3 (8)	4.2 ±0.6 (7)	4.5 ±0.8 (10)	2.0 ±0.5 (7)	1.0 ±0.6 (6)	2.9 ±0.5 (8)
August 1-15	2.5 ±0.3 (5)	n/a	0.4 (1)	n/a	0.8 ±0.03 (2)	3.3 ±1.4 (6)

[a] Sample size

Appendix B.1. Mean dead plant material (g/m^2) for successive cuttings in 1995 and 1996 (±1 S.E.). All 1995 samples were collected within exclosures that had been in place for the previous two weeks. In 1996, exclosures were used only on MB and MC to simulate the absence of cattle grazing. These exclosures were in place for two, four and six weeks previous to cutting for the fourth, fifth and sixth cuttings respectively.

Cut date[a]	MC	MB	HF
May31/95	**148.1** ±20.9 (20)[b]	**79.3** ±12.1 (20)	**270.5** ±16.1 (32)
June15/95	**79.7** ±11.1 (20)	**21.5** ±4.3 (20)	**280.9** ±20.9 (32)
June30/95	**77.0** ±9.6 (20)	**80.7** ±14.5 (20)	**256.4** ±18.9 (29)
July 15/95	**92.3** ±12.4 (13)	**41.6** ±7.9 (20)	**245.8** ±23.5 (32)
July 30/95	**75.3** ±9.4 (16)	**31.1** ±5.3 (19)	**171.1** ±14.8 (31)
Aug.14/95	**96.2** ±13.4 (16)	**39.3** ±5.4 (20)	**177.0** ±13.4 (32)
Mean of all cuttings	95.6 ±6.1 (105)	49.1 ±4.2 (119)	233.6 ±8.0 (188)

	Exclosure	No Exclosure	Exclosure	No Exclosure	Unburned	Burned[c]
May31/96	n\a	**121.1** ±21.4 (10)	n\a	**63.7** ±23.1 (10)	**313.0** ±30.5 (10)	**124.6** ±17.6 (10)
June15/96	n\a	**87.5** ±26.1 (10)	n\a	**73.1** ±17.2 (10)	**335.3** ±62.6 (10)	**86.4** ±28.8 (10)
June30/96	n\a	**80.5** ±19.2 (10)	n\a	**75.5** ±20.0 (10)	**208.8** ±33.6 (10)	**36.3** ±19.0 (10)
July 15/96	**67.3** ±11.8 (10)	**85.2** ±8.8 (10)	**42.4** ±11.2 (10)	**22.8** ±4.7 (10)	**204.1** ±38.4 (10)	**32.5** ±5.5 (10)
July 30/96	**109.0** ±9.8 (10)	**85.4** ±15.9 (10)	**114.3** ±15.5 (10)	**74.3** ±11.3 (10)	**158.0** ±25.1 (10)	**40.2** ±12.7 (10)
Aug.14/96	**124.1** ±18.9 (9)	**52.5** ±12.3 (9)	**63.4** ±13.4 (9)	**48.1** ±11.3 (9)	**199.2** ±21.9 (10)	**82.4** ±14.5 (10)
Mean of all cuttings	**99.3** ±8.8 (29)	**85.9** ±7.6 (59)	**73.7** ±9.5 (29)	**59.8** ±6.7 (59)	**236.4** ±17.0 (60)	**67.1** ±8.2 (60)

[a] Median date of cuttings. Sites clipped on three successive days.

[b] Sample size

[c] HF sample points were distributed evenly amongst areas burned on April 29/96 and unburned areas.

Appendix B.2. Mean digestible protein content (crude protein x digestibility) of grasses (%) for successive cuttings in 1995 and 1996 (±1S.E.). All 1995 samples were collected within exclosures that had been in place for the previous two weeks. In 1996, exclosures were used only on MB and MC to simulate the absence of cattle grazing. These exclosures were in place for two, four and six weeks previous to cutting for the fourth, fifth and sixth cuttings respectively.

Cut date[a]	MC		MB		HF	
May 31/95	11.0 ±0.5 (20)[b]		7.5 ±0.4 (20)		11.3 ±0.3 (31)	
June 15/95	7.0 ±0.2 (20)		6.3 ±0.2 (20)		8.6 ±0.4 (32)	
June 30/95	5.1 ±0.2 (20)		5.6 ±0.2 (20)		6.6 ±0.2 (28)	
July 15/95	4.2 ±0.1 (13)		5.0 ±0.2 (20)		5.4 ±0.2 (32)	
July 30/95	6.4 ±0.6 (16)		4.2 ±0.2 (19)		5.6 ±0.2 (31)	
August 14/95	8.7 ±0.6 (16)		5.1 ±0.2 (20)		5.1 ±0.2 (32)	
Mean of all cuttings	7.2 ±0.3 (105)		5.6 ±0.1 (119)		7.1 ±0.2 (186)	
	Exclosure	No Exclosure	Exclosure	No Exclosure	Unburned	Burned[c]
May 31/96	n/a	12.0 ±1.2 (10)	n/a	10.0 ±0.9 (6)	9.1 ±0.8 (10)	15.2 ±1.1 (6)
June 15/96	n/a	8.2 ±0.5 (10)	n/a	8.1 ±0.6 (10)	7.6 ±0.4 (10)	8.9 ±0.5 (10)
June 30/96	n/a	6.4 ±0.4 (10)	n/a	6.0 ±0.3 (10)	5.3 ±0.4 (10)	6.5 ±0.4 (10)
July 15/96	5.8 ±0.3 (10)	5.9 ±0.8 (10)	5.4 ±.0.3 (10)	5.2 ±.0.2 (7)	4.1 ±0.2 (10)	4.7 ±0.2 (10)
July 30/96	5.6 ±0.5 (10)	5.5 ±0.3 (9)	4.4 ±0.2 (10)	5.0 ±0.2 (10)	3.6 ±0.2 (10)	4.6 ±0.4 (10)
August 14/96	6.0 ±0.6 (9)	7.2 ±0.6 (7)	4.6 ±0.3 (9)	6.4 ±0.5 (7)	3.4 ±0.2 (9)	4.0 ±0.3 (10)
Mean of all cuttings	5.8 ±0.3 (29)	7.6 ±0.4 (56)	4.8 ±0.2 (29)	6.6 ±0.3 (50)	5.5 ±0.3 (59)	6.7 ±0.5 (56)

[a] Median date of cuttings. Sites clipped on three successive days.

[b] Sample size

[c] HF sample points were distributed evenly amongst areas burned on April 29/96 and unburned areas.

Appendix B.3. Mean digestible protein content (crude protein x digestibility) of forbs (%) for successive cuttings in 1995 and 1996 (±1S.E.). All 1995 samples were collected within exclosures that had been in place for the previous two weeks. In 1996, exclosures were used only on MB and MC to simulate the absence of cattle grazing. These exclosures were in place for two, four and six weeks previous to cutting for the fourth, fifth and sixth cuttings respectively.

Cut date[a]	MC	MB	HF
May 31/95	**16.6 ±0.4** (20)[b]	14.7 ±0.3 (20)	**14.8 ±0.7** (10)
June 15/95	**12.9 ±0.3** (20)	12.8 ±0.5 (20)	**12.6 ±1.8** (9)
June 30/95	**12.2 ±0.4** (20)	9.9 ±0.3 (20)	**10.9 ±1.5** (9)
July 15/95	**10.7 ±0.4** (13)	11.4 ±0.6 (20)	**9.8 ±0.6** (11)
July 30/95	**15.7 ±0.5** (16)	10.6 ±0.4 (19)	**10.4 ±0.8** (11)
August 14/95	**17.2 ±0.6** (16)	10.3 ±0.6 (20)	**8.7 ±0.6** (14)
Mean of all cuttings	**14.3 ±0.3** (105)	11.6 ±0.2 (119)	**11.0 ±0.5** (64)

	Exclosure	No Exclosure	Exclosure	No Exclosure	Unburned	Burned[c]
May 31/96	n/a	**23.6** ±1.2 (5)	n/a	**21.8** ±1.2 (4)	**7.80** (1)	**13.39** (1)
June 15/96	n/a	**17.7** ±0.2 (6)	n/a	**18.5** ±1.0 (8)	**13.2** ±2.7 (3)	**14.0** ±0.1 (2)
June 30/96	n/a	**15.8** ±0.3 (8)	n/a	**16.4** ±0.6 (7)	**8.6** ±1.0 (5)	**10.6** ±0.8 (4)
July 15/96	**13.0** ±0.4 (9)	**12.9** ±1.1 (6)	**12.3** ±0.8 (6)	**13.2** ±1.6 (5)	**8.2** ±0.8 (3)	**8.3** ±1.2 (5)
July 30/96	**13.0** ±0.8 (9)	**14.3** ±0.8 (5)	**10.6** ±0.8 (9)	**11.9** ±0.6 (6)	**6.2** ±1.2 (5)	**6.6** ±0.5 (4)
August 14/96	**10.9** ±1.1 (7)	**13.6** ±1.4 (3)	**10.0** ±0.7 (9)	**13.4** ±1.7 (4)	**6.4** ±1.0 (3)	**5.9** ±0.4 (5)
Mean of all cuttings	**12.4** ±0.5 (25)	**13.7** ±0.4 (33)	**10.8** ±0.5 (24)	**13.2** ±0.5 (34)	**8.3** ±0.7 (20)	**8.6** ±0.7 (21)

[a] Median date of cuttings. Sites clipped on three successive days.

[b] Sample size

[c] HF sample points were distributed evenly amongst areas burned on April 29/96 and unburned areas.

Appendix B.4. Mean digestible energy content (gross energy x digestibility) of grasses and forbs (kcal/g) for successive cuttings in 1995 (±1S.E.). All samples were collected within exclosures that had been in place for the previous two weeks.

Cutting date[a]	MC		MB		HF	
	Grass	Forb	Grass	Forb	Grass	Forb
May31	**2.55**	**3.02**	**2.09**	**2.94**	**2.42**	**2.76**
	±0.03	±0.04	±0.03	±0.04	±0.02	±0.12
	(20)[b]	(20)	(19)	(19)	(32)	(10)
June15	**2.01**	**2.87**	**2.06**	**2.95**	**2.30**	**2.61**
	±0.02	±0.02	±0.02	±0.03	±0.02	±0.05
	(20)	(20)	(20)	(18)	(32)	(11)
June30	**1.71**	**3.01**	**2.02**	**2.63**	**1.99**	**2.66**
	±0.01	±0.02	±0.02	±0.03	±0.02	±0.04
	(20)	(20)	(20)	(20)	(29)	(15)
July 15	**1.74**	**2.85**	**1.86**	**2.79**	**1.80**	**2.52**
	±0.02	±0.04	±0.02	±0.05	±0.01	±0.03
	(13)	(13)	(20)	(20)	(32)	(19)
July 30	**1.81**	**3.02**	**1.58**	**2.78**	**1.90**	**2.46**
	±0.05	±0.02	±0.01	±0.03	±0.02	±0.03
	(15)	(16)	(19)	(18)	(31)	(19)
August 14	**2.12**	**2.99**	**1.72**	**2.75**	**1.86**	**2.45**
	±0.03	±0.04	±0.02	±0.03	±0.01	±0.05
	(16)	(16)	(19)	(20)	(32)	(15)
Mean	**2.01**	**2.96**	**1.89**	**2.80**	**2.04**	**2.57**
of all	±0.03	±0.01	±0.02	±0.02	±0.02	±0.03
cuttings	(104)	(105)	(117)	(115)	(187)	(55)

[a] Median date of cuttings. Sites clipped on three successive days.

[b] Sample size

Appendix B.5. Mean total digestible protein content (digestible protein x biomass) of grasses (g/m^2) for successive cuttings in 1995 and 1996 (±1S.E.). All 1995 samples were collected within exclosures that had been in place for the previous two weeks. In 1996, exclosures were used only on MB and MC to simulate the absence of cattle grazing. These exclosures were in place for two, four and six weeks previous to cutting for the fourth, fifth and sixth cuttings respectively.

Cut date[a]	MC	MB	HF
May	8.9 ±1.0	3.9 ±0.6	6.2 ±0.8
31/95	(20)[b]	(20)	(32)
June	8.4 ±0.9	2.9 ±0.4	9.5 ±1.1
15/95	(20)	(20)	(32)
June	8.0 ±0.7	5.6 ±0.5	10.9 ±1.1
30/95	(20)	(20)	(29)
July	10.3 ±1.1	4.7 ±0.5	7.8 ±0.6
15/95	(13)	(20)	(32)
July	7.1 ±1.3	4.8 ±0.6	9.0 ±0.5
30/95	(16)	(19)	(31)
August	10.7 ±1.7	2.9 ±0.3	11.0 ±0.7
14/95	(16)	(20)	(32)
Mean of all cuttings	8.8 ±0.5 (105)	4.2 ±0.2 (119)	9.1 ±0.4 (188)

	Exclosure	No Exclosure	Exclosure	No Exclosure	Unburned	Burned[c]
May	n\a	11.2	n\a	2.7	4.1	2.4
31/96		±2.5		±0.7	±0.6	±0.4
		(10)		(10)	(10)	(10)
June	n\a	9.5	n\a	7.1	7.2	10.0
15/96		±1.4		±1.8	±1.3	±1.8
		(10)		(10)	(10)	(10)
June	n\a	12.9	n\a	6.7	8.2	9.5
30/96		±2.6		±1.1	±1.9	±1.1
		(10)		(10)	(10)	(1.10)
July	10.0	4.2	6.2	1.6	6.9	8.8
15/96	±1.7	±0.7	±1.6	±0.3	±1.3	±1.4
	(10)	(10)	(10)	(10)	(10)	(10)
July	8.4	3.3	7.7	3.2	7.5	9.0
30/96	±1.3	±0.6	±1.1	±0.4	±1.2	±1.0
	(10)	(10)	(10)	(10)	(10)	(10)
August	11.2	2.3	5.1	1.3	7.0	9.5
14/96	±1.7	±0.5	±1.1	±0.2	±1.4	±2.1
	(9)	(9)	(9)	(9)	(10)	(10)
Mean of	9.8	7.3	6.4	3.8	6.8	8.2
all	±0.9	±0.8	±0.7	±0.5	±0.6	±0.6
cuttings	(29)	(59)	(29)	(59)	(60)	(60)

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[a] Median date of cuttings. Sites clipped on three successive days.

[b] Sample size

[c] HF sample points were distributed evenly amongst areas burned on April 29/96 and unburned areas.

Appendix B.6. Mean total digestible protein content (digestible protein x biomass) of forbs (g/m^2) for successive cuttings in 1995 and 1996 (±1S.E.). All 1995 samples were collected within exclosures that had been in place for the previous two weeks. In 1996, exclosures were used only on MB and MC to simulate the absence of cattle grazing. These exclosures were in place for two, four and six weeks previous to cutting for the fourth, fifth and sixth cuttings respectively.

Cut date[a]	MC	MB	HF
May31/95	3.7 ±0.4 (20)[b]	1.8 ±0.2 (20)	0.5 ±0.2 (32)
June15/95	4.1 ±0.5 (20)	3.4 ±0.6 (20)	0.4 ±0.1 (32)
June30/95	7.8 ±0.8 (20)	3.4 ±0.4 (20)	0.8 ±0.3 (29)
July 15/95	4.7 ±0.5 (13)	3.5 ±0.4 (20)	0.5 ±0.2 (32)
July 30/95	4.9 ±0.6 (16)	2.6 ±0.4 (19)	0.6 ±0.3 (31)
Aug.14/95	4.0 ±0.7 (16)	1.5 ±0.2 (20)	0.5 ±0.2 (32)
Mean of all cuttings	4.9 ±0.3 (105)	2.7 ±0.2 (119)	0.5 ±0.1 (188)

	Exclosure	No Exclosure	Exclosure	No Exclosure	Unburned	Burned[c]
May31/96	n/a	2.4 ±0.5 (10)	n/a	1.9 ±0.4 (10)	0.3 ±0.2 (10)	0.2 ±0.1 (10)
June15/96	n\a	4.0 ±1.2 (10)	n\a	4.3 ±0.9 (10)	1.4 ±0.8 (10)	0.5 ±0.2 (10)
June30/96	n\a	6.6 ±1.7 (10)	n\a	4.1 ±1.1 (10)	1.6 ±0.8 (10)	1.4 ±0.5 (10)
July 15/96	5.4 ±1.1 (10)	2.9 ±0.7 (10)	4.4 ±1.1 (10)	1.9 ±0.4 (10)	1.2 ±0.5 (10)	2.0 ±0.7 (10)
July 30/96	5.6 ±0.9 (10)	2.4 ±0.5 (10)	6.3 ±1.3 (10)	2.7 ±0.7 (10)	1.7 ±0.7 (10)	1.2 ±0.7 (10)
Aug.14/96	4.5 ±1.5 (9)	0.7 ±0.2 (9)	4.6 ±0.5 (9)	1.2 ±0.3 (9)	0.8 ±0.3 (10)	1.4 ±0.5 (10)
Mean of all cuttings	5.2 ±0.7 (29)	3.2 ±0.4 (59)	5.1 ±0.6 (29)	2.7 ±0.3 (29)	1.2 ±0.2 (60)	1.1 ±0.2 (60)

[a] Median date of cuttings. Sites clipped on three successive days.

[b] Sample size

[c] HF sample points were distributed evenly amongst areas burned on April 29/96 and unburned areas.

Appendix B.7. Mean total digestible energy content (digestible energy x biomass) of grasses and forbs (kcal/m^2) for successive cuttings in 1995 (±1S.E.). All samples were collected within exclosures that had been in place for the previous two weeks.

Cutting date[a]	MC		MB		HF	
	Grass	Forb	Grass	Forb	Grass	Forb
May31	**202.59**	**67.39**	**105.21**	**37.77**	**134.46**	**9.38**
	±0.02	±0.01	±0.01	±0.01	±0.02	±0.01
	(20)[b]	(20)	(20)	(20)	(32)	(32)
June15	**232.14**	**92.63**	**95.91**	**75.67**	**244.16**	**7.88**
	±0.02	±0.01	±0.01	±0.01	±0.02	±0.01
	(20)	(20)	(20)	(20)	(32)	(32)
June30	**262.92**	**198.10**	**202.34**	**90.84**	**323.79**	**22.10**
	±0.02	±0.02	±0.02	±0.01	±0.03	±0.01
	(20)	(20)	(20)	(20)	(29)	(29)
July 15	**420.63**	**130.67**	**179.09**	**90.38**	**258.99**	**12.81**
	±0.04	±0.02	±0.02	±0.01	±0.02	±0.01
	(13)	(13)	(20)	(20)	(32)	(32)
July 30	**192.89**	**95.21**	**180.18**	**68.20**	**305.77**	**13.31**
	±0.02	±0.01	±0.02	±0.01	±0.02	±0.01
	(16)	(16)	(19)	(19)	(31)	(31)
August 14	**256.72**	**71.47**	**103.19**	**41.32**	**395.64**	**13.62**
	±0.03	±0.01	±0.01	±0.01	±0.02	±0.01
	(16)	(16)	(20)	(20)	(32)	(32)
Mean	**253.48**	**109.79**	**144.02**	**67.36**	**276.24**	**13.04**
of all	±11.75	±7.30	±7.49	±4.28	±10.09	±1.93
cuttings	(105)	(105)	(119)	(119)	(188)	(188)

[a] Median date of cuttings. Sites clipped on three successive days.

[b] Sample size

Appendix B.8. Pearson partial correlations between forage biomass and quality variables of forb and grass samples collected in 1995 and 1996 on all 3 sites. Each pair of variables was compared while controlling for the remaining variables. Data on gross energy were not collected in 1996. Significant correlations ($p<0.05$) shown in bold.

Grass samples from 1995 (n=174)

	Gross energy	Crude Protein	Digestibility
Biomass	0.03	0.012	**-0.18**
	p=0.73	p=0.88	p=0.017
Gross energy		**0.46**	-0.01
		p<0.001	p=0.93
Crude protein			**0.63**
			p<0.001

Forb samples from 1995 (n=143)

	Gross energy	Crude Protein	Digestibility
Biomass	0.06	**-0.34**	**0.27**
	p=0.50	p<0.001	p<0.001
Gross energy		0.12	-0.10
		p=0.14	p=0.25
Crude protein			**0.53**
			p<0.001

Grass samples from 1996 (n=251)

	Crude Protein	Digestibility
Biomass	**-0.17**	-0.07
	p=0.006	p=0.26
Crude Protein		**0.62**
		p<0.001

Forb samples from 1996 (n=152)

	Crude Protein	Digestibility
Biomass	-0.14	-0.002
	p=0.09	p=0.99
Crude Protein		**0.66**
		p<0.001

Appendix C.1 Mean rate of weight change (g/day) for adult (>1 year old) males during successive two week intervals in 1995 and 1996 (±1 S.E.). To calculate these values, the weight closest (±3 days) to the beginning of a specific interval was subtracted from the weight closest (±3 days) to the end of the interval for the same animal and the difference between these two weights was divided by the number of intervening days.

Year	Weight interval	Non-supplemented		Supplemented[a]	
		North	Road	Station	Gorge
1995	May 1-15	n/a	0.7 ±0.9	-0.6 ±1.0	2.9 ±2.1
			(6)[b]	(7)	(3)
	May 16-31	3.2 ±1.1	1.5 ±1.1	5.5 ±0.5	3.3 ±0.7
		(4)	(5)	(8)	(6)
	June 1-15	3.7 ±0.4	2.3 ±0.7	7.9 ±1.8	5.8 ±1.0
		(5)	(5)	(5)	(7)
	June 16-30	3.2 ±0.5	1.3 ±0.6	7.3 ±1.1	10.3 ±1.4
		(4)	(6)	(4)	(6)
	July 1-15	n/a	3.4 ±0.5	8.4 ±0.7	8.9 ±1.6
			(5)	(7)	(6)
	July 16-31	n/a	-0.8 ±2.0	3.8	5.9
			(2)	(1)	(1)
1996	May 1-15	-5.0	-2.4 ±0.9	-5.4 ±0.6	-4.3 ±0.8
		(1)	(6)	(9)	(5)
	May 16-31	3.1 ±1.5	0.9 ±0.7	3.3 ±0.7	2.4 ±0.5
		(4)	(7)	(12)	(9)
	June 1-15	2.8 ±0.1	2.9 ±0.6	5.8 ±0.7	3.6 ±1.1
		(3)	(6)	(9)	(5)
	June 16-30	1.8 ±0.7	1.7 ±1.4	9.0 ±1.3	6.0 ±0.9
		(3)	(4)	(4)	(5)
	July 1-15	6.4	7.1	6.4 ±1.6	6.2 ±0.8
		(1)	(1)	(6)	(5)
	July 16-31	4.8 ±0.6	6.4	6.6 ±1.3	3.3 ±0.8
		(2)	(1)	(7)	(4)
	August 1-15	1.5 ±2.0	n/a	2.6 ±0.8	3.7 ±1.0
		(3)		(6)	(4)

[a] Supplemented with rolled corn ad lib. from May 27 to August 16 in both years.
[b] Sample size.

Appendix C.2. Mean rate of weight change (g/day) for yearling males during successive two week intervals in 1995 and 1996 (±1 S.E.). To calculate these values, the weight closest (±3 days) to the beginning of a specific interval was subtracted from the weight closest (±3 days) to the end of the interval for the same animal and the difference between these two weights was divided by the number of intervening days.

Year	Weight interval	Non-supplemented		Supplemented[a]	
		North	Road	Station	Gorge
1995	May 1-15	n/a	n/a	4.4 (1)[b]	n/a
	May 16-31	3.4 ±2.0 (2)	5.4 (1)	9.7 ±1.0 (2)	4.6 (1)
	June 1-15	3.4 ±0.5 (3)	4.3 ±0.7 (2)	5.8 (1)	3.8 (1)
	June 16-30	2.4 ±0.6 (4)	0.0 (1)	11.5 (1)	7.9 (1)
	July 1-15	7.3 (1)	-2.0 (1)	8.5 ±1.1 (6)	n/a
	July 16-31	0.7 (1)	2.8 (1)	7.6 ±1.1 (4)	n/a
	August 1-15	2.7 (1)	n/a	7.0 ±1.6 (2)	11.7 (1)
1996	May 1-15	n/a	n/a	-0.6 ±0.1 (2)	n/a
	May 16-31	n/a	n/a	6.1 ±0.8 (6)	6.6 ±0.6 (2)
	June 1-15	5.4 (1)	n/a	6.3 ±0.6 (7)	6.5 ±1.4 (4)
	June 16-30	4.0 (1)	n/a	5.2 ±1.1 (4)	1.2 (1)
	July 1-15	n/a	n/a	7.2 ±0.8 (4)	n/a
	July 16-31	n/a	n/a	3.9 ±0.2 (2)	4.3 (1)
	August 1-15	-1.4 (1)	n/a	2.7 ±0.5 (2)	4.3 (1)

[a] Supplemented with rolled corn ad lib. from May 27 to August 16 in both years.

[b] Sample size

Appendix C.3 Mean rate of weight change (g/day) for yearling females during successive two week intervals in 1995 and 1996 (±1 S.E.). To calculate these values, the weight closest (±3 days) to the beginning of a specific interval was subtracted from the weight closest (±3 days) to the end of the interval for the same animal and the difference between these two weights was divided by the number of intervening days.

Year	Weight interval	Non-supplemented		Supplemented[a]	
		North	Road	Station	Gorge
1995	May 1-15	n/a	4.6 (1)[b]	7.1 (1)	n/a
	May 16-31	4.1 ±1.4 (2)	6.4 (1)	6.8 ±1.4 (3)	n/a
	June 1-15	3.3 (1)	-1.2 (1)	4.3 ±0.3 (2)	5.0 (1)
	June 16-30	0.5 (1)	1.1 ±0.4 (4)	6.2 (1)	4.7 (1)
	July 1-15	n/a	2.7 ±0.5 (2)	8.4 ±0.7 (3)	n/a
	July 16-31	0.2 ±2.2 (2)	0.9 (1)	6.0 (1)	n/a
	August 1-15	-0.1 ±0.3 (3)	-0.5 (1)	5.8 (1)	n/a
1996	May 1-15	n/a	n/a	n/a	n/a
	May 16-31	5.0 (1)	3.3 (1)	4.8 ±1.4 (3)	3.2 (1)
	June 1-15	4.7 ±0.3 (2)	3.2 ±0.2 (2)	5.1 ±0.5 (9)	6.3 ±3.8 (2)
	June 16-30	2.5 (1)	4.0 ±0.5 (2)	1.6 ±0.4 (7)	2.6 ±1.1 (3)
	July 1-15	2.8 (1)	2.3 (1)	2.4 ±1.3 (7)	n/a
	July 16-31	4.6 (1)	1.3 (1)	5.5 ±0.7 (7)	n/a
	August 1-15	1.7 (1)	5.9 ±0.9 (3)	4.7 (1)	n/a

[a] Supplemented with rolled corn ad lib. from May 27 to August 16 in both years.

[b] Sample size

Appendix C.4. Mean rate of weight change (g/day) for successive two week intervals in 1995 and 1996 for adult (>1 year old) non-reproductive females (±1 S.E.). To calculate these values, the weight closest (±3 days) to the beginning of a specific interval was subtracted from the weight closest (±3 days) to the end of the interval for the same animal and the difference between these two weights was divided by the number of intervening days.

Year	Weight interval	Non-supplemented		Supplemented[a]	
		North	Road	Station	Gorge
1995	May 1-15	n/a	4.5 ±0.1 (2)[b]	2.5 ±2.4 (3)	0.0 (1)
	May 16-31	5.2 ±1.3 (3)	2.4 ±2.1 (3)	6.0 ±0.9 (5)	2.8 ±2.4 (3)
	June 1-15	1.7 ±0.5 (7)	-0.2 ±1.0 (2)	3.5 ±0.6 (4)	3.0 ±1.0 (4)
	June 16-30	0.5 (1)	1.1 ±0.4 (4)	6.2 (1)	4.7 (1)
	July 1-15	4.3 (1)	2.0 ±1.4 (4)	8.2 ±0.5 (4)	8.6 ±0.1 (2)
	July 16-31	0.2 ±2.2 (2)	2.2 ±1.1 (3)	5.0 ±0.6 (3)	n/a
	August 1-15	-0.1 ±0.3 (3)	0.4 ±0.7 (4)	5.7 ±0.1 (2)	n/a
1996	May 1-15	0.3 ±0.3 (3)	-0.4 ±1.1 (2)	-3.4 ±0.8 (4)	-3.1 ±1.0 (3)
	May 16-31	5.1 ±0.9 (5)	4.6 ±0.9 (8)	3.1 ±1.0 (3)	5.9 ±2.1 (3)
	June 1-15	7.6 ±5.2 (6)	2.0 ±0.7 (10)	4.1 ±0.5 (3)	3.3 ±0.8 (4)
	June 16-30	2.9 ±0.6 (6)	-0.4 ±0.9 (6)	2.7 (1)	3.7 ±0.7 (4)
	July 1-15	3.8 ±0.5 (3)	3.6 ±0.7 (5)	n/a	5.0 (1)
	July 16-31	3.2 ±2.0 (4)	1.7 ±1.3 (2)	n/a	n/a
	August 1-15	-1.1 ±0.8 (2)	0.5 ±3.4 (2)	n/a	n/a

[a] Supplemented with rolled corn ad lib. from May 27 to August 16 in both years.
[b] Sample size

Appendix C.5. Mean rate of weight change (g/day) for successive two week intervals in 1995 and 1996 for adult (>1 year old) reproductive females (±1 S.E.). To calculate these values, the weight closest (±3 days) to the beginning of a specific interval was subtracted from the weight closest (±3 days) to the end of the interval for the same animal and the difference between these two weights was divided by the number of intervening days.

Year	Weight interval	Non-supplemented		Supplemented[a]	
		North	Road	Station	Gorge
1995	May 1-15	n/a	n/a	1.1 ±1.1 (3)[b]	5.3 (1)
	May 16-31	-0.2 ±3.5 (2)	4.5 ±0.9 (2)	5.0 ±1.7 (2)	0.6 ±1.4 (2)
	June 1-15	-0.3 ±1.0 (5)	-4.3 (1)	2.9 ±0.5 (2)	1.7 ±0.0 (2)
	June 16-30	-5.1 ±0.6 (5)	-2.3 ±0.1 (2)	0.1 ±0.8 (4)	-1.9 ±1.0 (2)
	July 1-15	3.8 ±0.9 (5)	1.7 ±0.2 (3)	-0.1 ±0.8 (7)	4.8 ±1.1 (3)
	July 16-31	1.0 ±0.8 (5)	0.9 (1)	9.1 ±0.4 (2)	n/a
	August 1-15	0.8 (1)	0.8 (1)	n/a	n/a
1996	May 1-15	-0.4 ±0.2 (2)	n/a	-3.4 ±0.8 (4)	0.5 (1)
	May 16-31	6.1 ±1.3 (6)	4.5 ±1.5 (3)	2.5 ±0.8 (10)	4.5 ±2.3 (3)
	June 1-15	-0.4 ±0.5 (5)	2.2 ±0.5 (4)	1.8 ±0.6 (13)	-0.6 ±1.0 (3)
	June 16-30	-0.8 ±0.4 (5)	1.0 ±0.9 (3)	-1.0 ±0.4 (14)	1.5 ±0.2 (2)
	July 1-15	0.6 ±1.1 (4)	-0.8 ±0.6 (3)	3.2 ±1.2 (12)	2.8 ±1.1 (2)
	July 16-31	2.8 ±0.8 (4)	3.1 ±0.6 (4)	4.3 ±1.2 (6)	4.8 ±0.4 (2)
	August 1-15	1.2 ±1.4 (3)	5.4 ±1.9 (3)	2.1 (1)	n/a

[a] Supplemented with rolled corn ad lib. from May 27 to August 16.

[b] Sample size

Appendix D.1. Mean (± 1 S.E.) concentration (mg/g) and ratios of long chain alkanes in forb and grass samples collected from MB and MC in 1995. Samples were collected over 2 consecutive days during each cutting period from wire mesh exclosures that were in place for two weeks previous to the cutting date.

Cut period	Alkane	MC		MB	
		Forb	Grass	Forb	Grass
June 14-15	C_{29}	**0.109** ±0.022 (5)[a]	**0.196** ±0.031 (5)	**0.199** ±0.034 (4)	**0.193** ±0.039 (5)
	C_{31}	**0.069** ±0.011 (5)	**0.228** ±0.039 (5)	**0.140** ±0.030 (4)	**0.300** ±0.059 (5)
	C_{33}	**0.011** ±0.002 (5)	**0.043** ±0.009 (5)	**0.027** ±0.014 (4)	**0.061** ±0.012 (5)
	$C_{29} : C_{31}$	**1.59**	**1.40**	**1.43**	**0.64**
	$C_{31} : C_{33}$	**6.31**	**5.32**	**5.15**	**4.95**
	$C_{29} : C_{33}$	**10.01**	**4.57**	**7.35**	**3.18**
June 29-30	C_{29}	**0.140** ±0.018 (5)	**0.287** ±0.010 (5)	**0.146** ±0.018 (3)	**0.162** ±0.014 (5)
	C_{31}	**0.076** ±.008 (5)	**0.364** ±0.016 (5)	**0.057** ±0.105 (3)	**0.287** ±0.031 (5)
	C_{33}	**0.010** ±0.001 (5)	**0.062** ±0.006 (5)	**0.011** ±0.066 (3)	**0.064** ±0.006 (5)
	$C_{29} : C_{31}$	**1.85**	**0.79**	**2.55**	**0.57**
	$C_{31} : C_{33}$	**7.27**	**5.88**	**5.31**	**4.49**
	$C_{29} : C_{33}$	**13.42**	**4.65**	**13.53**	**2.54**
July 14-15	C_{29}	**0.099** ±0.038 (2)	**0.186** ±0.026 (6)	**0.112** ±0.012 (6)	**0.137** ±0.022 (5)
	C_{31}	**0.059** ±0.006 (2)	**0.310** ±0.039 (6)	**0.106** ±0.032 (6)	**0.287** ±0.026 (5)
	C_{33}	**0.008** ±0.001 (2)	**0.062** ±0.013 (6)	**0.015** ±0.023 (6)	**0.065** ±0.008 (5)
	$C_{29} : C_{31}$	**1.67**	**0.60**	**1.05**	**0.48**
	$C_{31} : C_{33}$	**7.59**	**5.00**	**7.27**	**4.41**
	$C_{29} : C_{33}$	**12.68**	**3.00**	**7.64**	**2.10**
July 30-31	C_{29}	**0.039** ±0.007 (5)	**0.220** ±0.041 (4)	**0.144** ±0.012 (5)	**0.179** ±0.028 (5)
	C_{31}	**0.031** ±0.002 (5)	**0.336** ±0.064 (4)	**0.095** ±0.045 (5)	**0.279** ±0.029 (5)
	C_{33}	**0.005** ±0.001 (5)	**0.050** ±0.008 (4)	**0.026** ±0.025 (5)	**0.065** ±0.007 (5)
	$C_{29} : C_{31}$	**1.24**	**0.65**	**1.51**	**0.64**
	$C_{31} : C_{33}$	**6.00**	**6.71**	**3.65**	**4.30**
	$C_{29} : C_{33}$	**7.44**	**4.40**	**5.52**	**2.76**

[a] Sample size