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Some Morphological and Chemical Responses of Blackbrush (Coleogyne ramosissima) to Goat Browsing: Influences on Dietary Blackbrush Selection by Goats and Cattle

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SOME MORPHOLOGICAL AND CHEMICAL RESPONSES OF BLACKBRUSH (*COLEOGYNE RAMOSISSIMA*) TO GOAT BROWSING: INFLUENCES ON DIETARY BLACKBRUSH SELECTION BY GOATS AND CATTLE

by

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Frederick D. Provenza

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ABSTRACT

Some Morphological and Chemical Responses of Blackbrush *(Coleogyne ramosissima)* to Goat Browsing: Influences on Dietary Blackbrush Selection by Goats and Cattle

by

Frederick D. Provenza, Doctor of Philosophy

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Department: Range Science

Domestic goats were used to modify the growth form of blackbrush, a spinescent shrub occurring in nearly monospecific stands on several million hectares of rangeland in the southwestern United States. The objective of this research was to evaluate goat browsing as a means of improving these rangelands for cattle. Winter goat browsing stimulated spring twig growth from basal and axillary buds which resulted in increased production.

Twig production by heavily browsed plants (>95 percent removal of current season's twigs) was a function of precipitation, soil depth, branch location on the plant, and period of rest after browsing. As precipitation doubled, production increased by a factor of 1.9. Twig production by plants growing on deep soils (71 cm) was

1.9 times that by plants growing on shallow soils (39 cm). Older branches growing on the outer edges of blackbrush plants (terminal branches) produced 4.6 times more current season's twigs than sprouts and young branches (basal branches) growing within the shrub canopy. Heavily browsed plants increased twig production by a factor of 3.6 relative to control plants, and production remained at this level, even after four consecutive years of browsing. Stocking intensities of 2.4 animal-unit-months$\cdot$hectare^{-1} were required to achieve utilization levels of 80 percent in blackbrush pastures. Annual twig production declined with rest from browsing. However, plants which were browsed and subsequently rested for two years yielded an aggregate 1.6 times more available forage than plants which were browsed on a yearly basis. This was due to an accumulation of twigs ranging in age from one to three years.

Browsing also improved the apparent nutritional quality of blackbrush twigs. Current season's twigs contained more crude protein (6.5 versus 4.6 percent), phosphorus (0.10 versus 0.08 percent), and in vitro digestible dry matter (48 versus 38 percent) than older twigs. Current season's twigs from basal branches contained more crude protein (6.1 versus 5.7 percent) and in vitro digestible dry matter (44 versus 41 percent) than those from terminal branches.

The palatability of current season's twigs to goats and cattle was lower, however, than that of older twigs, presumably due to their higher tannin levels. Within individual blackbrush plants, current season's twigs from terminal branches were higher in tannins than those from basal branches. Rest from browsing resulted in decreased tannin levels due to a decrease in the proportion of

current season's to older twigs. Goats and cattle tended to prefer older twigs to current season's twigs, and current season's twigs from basal branches to those from terminal branches. The occurrence and allocation of tannins within blackbrush support hypotheses dealing with the elaboration and allocation of phyto-chemicals as defense mechanisms countering herbivory.

Esophageally fistulated goats (does and kids) browsing in pastures where forage consisted primarily of current season's twigs consumed diets with more crude protein, in vitro digestible dry matter, and tannins than goats browsing in pastures where forage consisted primarily of older twigs. They also lost less weight. Does initially consumed diets higher, but later consumed diets lower in crude protein than those consumed by kids. Kids consumed diets with more in vitro digestible dry matter, but lost more weight than does.

No statistically significant differences in weight response were recorded for cattle browsing in pastures which were, and were not, previously browsed by goats. However, the average heifer in previously unbrowsed pastures consumed 1.9 times more protein supplement than her counterpart in previously browsed pastures.

(166 pages)

INTRODUCTION

Significance and Statement of the Problem

Blackbrush (*Coleogyne ramosissima*) is a densely branched shrub, averaging less than one meter in height, which occurs on several million hectares of rangeland in the southwestern United States (Figure 1). Blackbrush occupies the transition zone between the Mojave and Great Basin deserts (Beatley 1975), and its distribution is apparently temperature limited (Wallace et al. 1970). Over much of the area this plant forms essentially pure stands, and associated grasses, forbs, and shrubs are rare (Humphrey 1953, Bowns 1973).

The terminal twigs of blackbrush branches tend to die back for several centimeters from the tip resulting in a spinescent growth form (Bowns 1973). Death of terminal buds suppresses apical dominance which allows lateral twig development, and as a result gives the shrub a round, compacted canopy. These factors limit the accessibility and palatability of blackbrush twigs for most ungulates and, consequently, this species is generally considered poor forage.

Humphrey (1953, 1955) considered blackbrush poor forage during spring, summer, and fall for cattle, but fair forage for goats during these seasons. In winter, when other feed was scarce, he rated it as fair forage for cattle. Sampson and Jespersen (1963) rated the shrub good to poor forage for goats and poor forage for cattle on California rangelands. On southern Utah ranges, the U.S. Forest

Figure 1. Map of blackbrush distribution according to Bowns and West (1976).

Service (1937) considered blackbrush fair forage for cattle during the winter, and Bowns and West (1976) considered it fair winter and spring forage for cattle and sheep. Research by Bradley (1965) and Wilson (1967), however, indicated the importance of the species to desert bighorn sheep, and Leach (1956) found it an important contributor to the winter diets of mule deer. Bowns and West (1976) indicated that the greatest economic use of blackbrush-dominated rangelands in Utah was winter browsing by mule deer and desert bighorn sheep, and winter and spring livestock browsing.

Nutritionally, blackbrush is low in crude protein and phosphorus. Crude protein levels cited by Bowns and West (1976) for material harvested in February and May were 7.3 and 8.8 percent for leaves versus 4.1 and 3.8 percent for stems, respectively; phosphorus content was 0.11 and 0.14 percent for leaves versus 0.10 and 0.13 percent for stems, respectively. Intact samples collected during January and February by Provenza (1977) averaged 4.6 percent crude protein and 0.16 percent phosphorus.

Domestic goats were used to modify the growth form of blackbrush in southwestern Utah in an attempt to improve these rangelands for cattle (Provenza 1977). Winter removal of spinescent material by goat browsing stimulated spring sprouting from basal and axillary buds. Heavily browsed plants produced large quantitites of new twigs which were more accessible and possibly more palatable and nutritious than woody material on unbrowsed plants.

Herbivores generally prefer new growth to older growth and new growth is generally more nutritious (Arnold 1964). For example, Reynolds and Sampson (1943) showed that the nutritive value and palatability of regrowth plant material in chaparral species was higher than that of older plant material. Nonsystematic observations of goats browsing blackbrush plants, however, suggested that the palatability of new twigs was lower than that of older twigs. A review of the literature indicated the decreased palatability of new twigs might be attributed to secondary compounds, and subsequent laboratory analyses confirmed that blackbrush contained high tannin levels.

The possibility that new growth is unpalatable to goats and cattle has practical, as well as theoretical, implications. From the management standpoint, subsequent use of previously browsed areas by goats and cattle would be possible only by fencing these areas, and the decreased palatability of new growth might decrease voluntary intake and animal performance.

Decreased palatability has been shown to be associated with toxic (alkaloids) or digestibility-reducing (tannins) compounds found in the new growth of some plant species. As Rhoades (1979) indicated, taste is a proximate sensation whose ultimate goal, determined over evolutionary time, is to protect the animal from ingesting harmful foods. However, as Arnold and Maller (1977) pointed out, taste evolved by an animal species in one area may not apply when that species is domesticated and introduced to continents with different botanical composition. Hence, determining the relative palatability of new versus old blackbrush twigs to goats and cattle and the causative factor(s) is of primary concern. Also, a nutritional comparison of new and old growth is important for guiding management decisions relative to supplementation.

From a theoretical standpoint, a growing body of literature indicates the importance of plant secondary compounds, as well as growth forms, as plant defenses against herbivory (Rosenthal and Janzen 1979). General hypotheses relative to plant antiherbivore strategy have been formulated based primarily on studies of plant-insect interactions. How these hypotheses relate to large herbivores in rangeland situations is unknown. The blackbrush plant community is an ideal location for elucidating plant secondary chemical and morphological responses to browsing, and also provides the opportunity for observing goat and cattle diet selection from a single woody plant species.

Purpose and Objectives

In the early 1900's blackbrush rangelands in southwestern Utah were browsed by domestic goats. Subsequent changes in land-use policy, coupled with consumer demands for beef, eventually resulted in these areas being used primarily as winter and spring ranges for cattle. With the current encroachment by an expanding human population, however, common use of rangelands by species whose food habits are complementary will be increasingly important. With its preference for woody vegetation, the goat has the potential for complementing species such as cattle that tend to prefer herbaceous vegetation, and blackbrush rangelands may be more suited to goat, rather than cattle, production.

Jenson et al. (1960) set the stocking rate for blackbrush ranges in southern Nevada at 0.08 to 0.04 animal-unit-months$\cdot ha^{-1}$, yet total available blackbrush forage in southwestern Utah has been estimated at 1513 kg$\cdot ha^{-1}$. This apparent discrepancy is partially a result of the compacted, spinescent growth form which reduces the accessibility and palatability of blackbrush twigs for cattle. The purpose of this study was to provide data on the responses of blackbrush, goats, and cattle to a biological manipulation program in which goats were used to improve blackbrush rangeland for cattle.

To quantify the effects of browsing on blackbrush the following objectives were proposed:

1. To determine the effects of four levels of stocking with goats (early January to mid-March of 1978 and 1979) and cattle (October 1979) upon the degree of utilization of blackbrush.

2. To assess the relationship between different utilization levels imposed by goats and subsequent production of current season's twigs by blackbrush branches.

3. To determine the effects of soil depth and stoniness, branch location, and utilization followed by rest upon the production of current season's twigs by heavily browsed blackbrush plants.

4. To determine the nutrient content (crude protein and phosphorus) and in vitro dry-matter digestibility of current season's

versus older twigs harvested from browsed versus unbrowsed blackbrush plants growing on deep and shallow soils.

5. To determine the effects of soil depth and stoniness, branch location, and utilization followed by rest upon the tannin levels of blackbrush twigs.

To quantify the nutritional status of goats browsing blackbrush pastures the following objectives were proposed:

1. To determine the botanical and chemical (crude protein, in vitro dry-matter digestibility and tannin) composition of the diets of esophageally fisulated does and kids browsing blackbrush pastures at two stocking intensities during the winter of 1979.

2. To determine the percent of time does and kids spent browsing at two stocking intensities during the winter of 1979.

3. To determine the body weight responses of does and kids browsing blackbrush pastures during the winter of 1979.

4. To determine the body weight responses of goats browsing at three stocking intensities to supplementation (protein and energy) during the winter of 1978.

To quantify the nutritional status of cattle browsing blackbrush pastures which were, and were not, previously browsed by goats, the following objectives were proposed:

1. To determine the botanical and chemical (crude protein, in vitro dry-matter digestibility and tannin) composition of diets from hand-plucked samples which simulated twigs consumed by cattle browsing blackbrush pastures.

2. To determine the percent of time that cattle in blackbrush pastures spent browsing.

3. To determine the body weight response of protein supplemented cattle browsing blackbrush pastures.

4. To determine the quantity of protein supplement consumed by cattle browsing blackbrush pastures.

REVIEW OF LITERATURE

Response of Blackbrush to Goat Browsing

Morphological

The quantity and quality of solar radiation, air and soil temperature, soil type and depth, and available soil moisture are important in determining the annual production of shrubs. Annual fluctuations in environmental factors may result in increased or decreased productivity, depending on individual species optima and the extent of the fluctuations. Wallace et al. (1970), for example, compared root and shoot production at three soil temperatures of 13 shrub species which grow in the transitional area between the Mojave and Great Basin deserts. The production of individual blackbrush seedlings was greatest at 21°C (0.20 g roots, 1.93 g shoots) and decreased at 16°C (0.09 g roots, 0.81 g shoots) and 28°C (0.08 g roots, 0.58 g shoots). Bowns (1973) presented data suggesting the rate of twig growth by blackbrush was greatest at air temperatures of 20-30°C, provided adequate soil moisture was available; at air temperatures greater than 30°C or less than 20°C, the rate of twig growth was depressed. Soil temperatures, which were affected by air temperatures, showed a similar correlation with the rate of twig growth. Depletion of available soil moisture, however, was the overriding factor in determining growth rate (Bowns 1973), and summer dormancy of blackbrush is a result of low soil moisture rather than high temperatures (Wallace and Romney 1972).

Twig growth is affected by branch location within the plant. Bowns (1973) indicated that the average annual growth for blackbrush twigs on terminal, lateral, and basal branches was 13, 10, and 25 mm in 1970 and 24, 9, and 43 mm in 1971. Rains during May of 1971 were responsible for the increased twig production. He stated that there was a tendency for terminal twigs to die after a few years, dry up for several centimeters back from the tip and become spinescent. Death of terminal buds suppresses apical dominance which allows lateral twig development and results in the round, compacted growth form typical of blackbrush.

Another important factor in determining the growth response of shrubs is twig removal, which may have a stimulating or depressing effect on twig production. Environmental factors, season and degree of twig removal, apical dominance, and twig location within the plant interact to determine the ultimate response of shrubs to twig removal.

In general, unbrowsed shrubs produce less twig growth because browsing removes the apical bud allowing increased twig production by lateral branches. *Purshia tridentata* (Martinson 1960, Garrison 1953, Ferguson and Basile 1966), *Cercocarpus ledifolius* (Thompson 1970, Garrison 1953), *Cercocarpus montanus* (Smith 1955), *Chrysothamnus nauseosus* (Garrison 1953), *Chrysothamnus viscidiflorus* (Willard and McKell 1978, Tueller and Tower 1979), *Symphoricarpos* spp. (Willard and McKell 1978, Price 1941), *Amelanchier alnifolia* (Young and Payne 1948), and *Coleogyne ramosissima* (Provenza 1977, Bowns 1973), to name a few, were stimulated by twig removal. Each species, however, reacted differently depending on the season and intensity of twig removal and overutilization may harm the plants. Cook (1971), for example, reported that removal of greater than 50 percent of the current season's twigs from desert shrubs in late spring and summer for three years reduced yields, and many plants were killed by 90 percent removal.

Shrubs which are browsed and subsequently rested show initial increases in twig production followed by stagnation. Davis (1953) reported increased growth of several shrub species during the initial year of herbage removal, but noted a decline in production unless clipping was continued. Tueller and Tower (1979) presented examples of decreased twig production resulting from the lack of twig removal, and Ellison (1960) discussed this subject in his review of the influence of grazing on plant succession.

Chemical

Nutritionally, blackbrush is low in crude protein and phosphorus during the dormant season. Crude protein levels cited by Bowns (1973) for material harvested in November and February averaged 7.4 percent for leaves and 3.1 percent for stems, and phosphorus levels averaged 0.11 percent for leaves and 0.10 percent for stems. Provenza (1977) presented data suggesting an inverse relationship between body weight loss and percent crude protein ($r^2 = 0.91$) in the hand-plucked diets of Angora goats browsing blackbrush pastures during winter. Body weight loss varied from 19.5 to 11.6 percent corresponding with crude protein levels that varied from 4.2 to 5.1 percent. Wallace and Romney (1972) found that phosphorus content of blackbrush ranged from 0.06 to 0.20 percent for stems and 0.07 to 0.28 percent for leaves, depending on soils and location. Phosphorus levels cited by Provenza (1977) averaged 0.15 to 0.18 percent for plants growing on shallow and deep soils, respectively.

Huston et al. (1971) recommended a minimum of 9.0 percent crude protein and 0.16 percent phosphorus in the diets of Angora goat wethers and dry does for a medium level of production; requirements for pregnant and lactating does, developing billies, kids, and yearlings were higher. Lower crude protein levels would probably be acceptable for short-hair goats, however, due to their lower requirements for hair growth. Cook and Harris (1968) recommended a diet containing 4.4 percent digestible protein and 0.17 percent phosphorus for cattle and sheep during gestation, with higher requirements for lactation.

Provenza (1977) found increased crude protein and phosphorus levels for blackbrush plants growing in deep versus shallow soils and suggested enhanced soil moisture relations on deeper soils as a possible explanation. Available soil moisture, temperature, soil type, site, and general climatic conditions have all been shown to influence the chemical composition of plants. The effects of soil variables on plant nutritive content are difficult to evaluate, however, because of interdependent factors including soil acidity, soil moisture, structure, texture, organic-matter content, soil organisms, and the chemical composition of the soil solution (Cook and Harris 1950).

Daniel and Harper (1934) concluded that the study of a single nutrient element in the soil did not give a reliable indication of the amount of that element in the plant, since many soil factors were involved and plant species varied in their ability to utilize soil nutrients. Cook and Harris (1950) concluded that environmental factors and soil moisture were more important in determining the nutrient content of range plants under various site conditions (slope, exposure, vegetation cover) than the chemical content of the soil. Nevertheless, Stoddart (1941) found that snowberry (*Symphoricarpos rotundifolius*) plants grown on various soil types showed marked differences in ash, protein, and phosphorus content, and Midgley (1937) indicated that soils with high mineral content produced plants high in minerals. Stoddart et al. (1975) concluded from a review of the literature that good sites and growing conditions produced good forage.

Although environmental factors are important, twig age often accounts for larger differences in the chemical composition of shrubs. The nutritional quality of current season's twigs varies with developmental stage and as twigs age crude protein and phosphorus levels decline while fiber levels increase (Halls and Alcaniz 1972, Reynolds 1967, Aldous 1945, Reynolds and Sampson 1943). Bowns and West (1976) stated that crude protein levels for blackbrush stems collected in May during the growing season were 3.8 percent while crude protein levels for stems collected in November during the dormant season were 2.2 percent; phosphorus levels for May and November were 0.13 and 0.10 percent while acid detergent fiber levels were 45.3 and 52.2 percent, respectively. Chatterton et al. (1971) showed levels of crude protein, phosphorus, and fiber in *Atriplex* *polycarpa* varied seasonally, but even greater differences existed for new versus old (older than 1 year) twigs. In their study, seasonal ranges for new and old growth, respectively, were from 10-13 and 6-10 percent for crude protein, from 0.08-0.12 and 0.05-0.08 percent for phosphorus, and from 28-35 and 42-50 percent for fiber.

Factors that relate to a shrub's chemical make-up include primary plant metabolites such as nitrogen, as well as secondary plant metabolites such as tannins. Both primary and secondary plant metabolites influence the productivity of ruminants by affecting forage (nutrient) intake. Low nitrogen levels, typical of blackbrush, suppress microbial activity in the rumen thereby decreasing fiber digestibility and lowering forage intake (Moir and Harris 1962, van Glyswyk 1970). High tannin levels, also typical of blackbrush, depress intake levels by decreasing palatability (Arnold et al. 1980, McLeod 1974), and suppressing protein and fiber digestion in the rumen (McLeod 1974).

Secondary compounds, such as tannins in plants, have probably evolved as chemical defenses against herbivory (Rosenthal and Janzen 1979). Two lines of evidence have been used to show anti-herbivore activity by secondary compounds. The first involves deterrency (decreased palatability) while the second involves anti-biosis (decreased herbivore fitness).

Tannins deter herbivores by their protein-complexing activities. During mastication, tannins form insoluble complexes with plant proteins (Swain 1979), and also tan the proteinaceous mucosal membranes of the mouth. The resultant astringent sensation experienced by human beings, and presumably large herbivores (Arnold et al. 1980), is probably a result of the protein-complexing properties of tannins (Rhoades 1979). Because of this, some herbivores have evolved oral and nasal receptor systems capable of detecting tannins in plants and the ensuing ability to react negatively to signals from these receptors. The undesirable taste and odor, however, are evolved responses to the negative effect tannins have on forage digestibility and therefore animal fitness (Rhoades 1979).

Some debate exists concerning the role(s) of secondary compounds, and as McKey (1979) indicated, multiple functions (metabolic and ecological) are to be expected. Early workers, however, were unable to assign a definite metabolic role to alkaloids and concluded they were plant waste products. Some alkaloid biochemists recently concurred with this evaluation and the "waste product hypothesis" was expanded to include plant secondary compounds in general (Rhoades and Cates 1976). Evidence for the metabolic significance of secondary metabolites has accumulated recently, however, and these substances have been implicated as storage compounds and regulators of plant metabolism and growth (del Moral 1972, Galbraith et al. 1972, Arntzen et al. 1974, McClure 1975, Seigler 1977). The majority of cases in which adaptive significance has been demonstrated for secondary compounds, however, concern ecological interactions between plants and their associated biota (Rosenthal and Janzen 1979), and Laycock (1978) discussed this subject in relation to large herbivores on rangelands.

The increasing evidence for the significance of secondary compounds in plant defense against herbivory has led to the development of hypotheses based on an optimal defense strategy by plants (Rhoades 1979). Fundamental to these hypotheses is the principal of resource allocation based on the assumption that resource budgets are limited (Haukioja 1980). The concept of costs and benefits of defense is central to hypotheses postulating variations in defense investment, but to date no quantitative data exist concerning cost-benefit interactions within plants (McKey 1979).

Empirical evidence suggests production of secondary compounds imposes a metabolic cost to the plant and the amount produced is a variable and heritable trait. Cates (1975) measured the difference in growth rate and reproductive output between different morphs in a plant population polymorphic for chemical defenses and found, in the absence of herbivory, the palatable morph lacking the chemical deterrent had higher growth rates and produced more seeds than the unpalatable morph possessing the deterrent.

Artificial selection has resulted in increased or decreased concentrations of secondary compounds such as tannins in *Sorghum* grain (Stitt 1943, Harris et al. 1970), indicating these compounds are sufficiently variable and heritable for natural selection to act upon. Little is known, however, about the genetic basis for variation in secondary compound production within and among plants of a given species.

Rhoades (1979) presented four hypotheses central to a theory of optimal defense of plants against herbivores:

1. The first hypothesis states plants evolve defenses in direct proportion to the risk of herbivory and in inverse proportion to the cost of defense. Plants are generally divided into two groups, unapparent and apparent (Feeny 1976), based on their likelihood of being consumed by an herbivore. Chemical defenses of unapparent plants (qualitative defenses) tend to be present in low concentrations interfering with the internal metabolism of herbivores, while defenses of apparent plants (quantitative defenses) tend to be present in high concentrations reducing the digestibility of plant tissues (Rhoades and Cates 1976). Unapparent plants tend to evolve defenses such as alkaloids which are less costly to produce, but can be circumvented by specialized herbivores that have evolved detoxification or tolerance mechanisms. Apparent plants tend to evolve defenses, such as tannins, which are more costly to produce but not easily circumvented by herbivores, due to their generalized protein-complexing abilities (Feeny 1975, Rhoades 1979). Swain (1979), however, indicated that during the course of the growing season, costs for unapparent (alkaloids) and apparent (tannins) plant defenses may be equal due to the rapid turnover of the former compounds relative to the latter.

Characteristics of unapparent versus apparent plants or plant parts are annual versus woody perennial species, early successional versus climax species, rare versus common species, young versus mature leaves, leaves versus bark and stems, and deciduous versus evergreen leaves. Blackbrush is an apparent plant and as such would be expected to contain high levels of digestion reducing substances such as tannins. Approximately 80 percent of woody perennial dicotyledonous plant species contain tannins as opposed to 15 percent of annual and herbaceous perennial dicot species (Bate-Smith and Metcalf 1957, Rhoades and Cates 1976).

2. The second hypothesis states that, within plants, defenses are allocated in direct proportion to the risk of the particular plant tissue to herbivory and the value of that tissue in terms of fitness loss to the plant resulting from herbivory, and in inverse proportion to the cost of defending the plant part. Four factors influencing within-plant defense allocation have been discussed in the literature and were summarized by McKey (1979): 1) costs of herbivory to different plant parts, 2) probability of discovery and successful herbivore attack in the absence of chemical defenses, 3) physiological constraints, and 4) distribution of other chemical defenses within the plant.

These four factors probably interact to determine the level(s) of secondary compound(s) within plant tissues and the risk of herbivory. Different plant parts (old vs. young leaves, leaves vs. stems, sun vs. shade leaves) have different photosynthetic rates and carbon export levels, and those parts which contribute less should be protected to a lesser degree. Some plant parts may be more difficult to defend than others due to morphological differences, and Orians and Janzen (1974) discussed the possibility that immature tissues may face constraints in production and storage of secondary compounds. Each plant part also has a discovery rate by herbivores which depends on phenology, density, location, and herbivore(s). If a plant part is discovered, mechanical defenses such as silica, calcium carbonate, and spinescence, as well as one or more types of chemical defense, influence herbivory.

3. The third hypothesis states that since defenses are costly, commitment to defense is decreased when herbivores are absent and increased when plants are subjected to herbivory. Rhoades (1979) presented several examples of increased levels of secondary compounds in response to herbivory. Induction times for defensive reactions range from 12 hours to 1 year. Qualitative defenses typical of unapparent plants are induced quickly, presumably because they are synthesized at less cost to the plant, are readily translocated to the site of damage, and are effective at low concentrations (Rhoades 1979). Quantitative defenses typical of apparent plants are induced slowly, presumably because larger quantities of materials must be synthesized and much of this synthesis must take place at the site of damage, since polymeric compounds like tannins are not known to be transported. Relaxation times for defensive reactions range from 18 days to 4 or 5 years, but data on this subject are limited.

McKey (1979) addressed the question of metabolism and catabolism of secondary compounds to molecules of value in primary metabolic pathways. Recent studies show that plants can degrade the A-ring of flavonoids to CO_2, but whether plants can catabolize tannins is questionable (Barz and Hösel 1975). The "disappearance" of tannins from plants is likely due to their increased polymerization to compounds of high molecular weight (Goldstein and Swain 1963, Joslyn and Goldstein 1964).

McKey (1979) stressed the fundamental biochemical similarities between plant and animal metabolism and the conflicts which arise as a result. Compounds readily metabolized by plants are potentially subject to metabolism by herbivores, and compounds resistant to metabolism by herbivores are probably refractory to plant enzymes.

4. The fourth hypothesis states that since plant defenses are costly, commitment to defense is a positive function of the total carbon and nutrient budget of the plant, and is inversely related to the carbon and nutrient allocation by the plant to other processes. Rhoades (1979) hypothesized that physical stress to plants (nutrient-poor soils, drought, competition, disease) results in an increase in their proximate nutritional quality to herbivores, particularly nitrogen and carbohydrate levels, and a decrease in the quantity and quality of their defensive systems. If plants possess qualitative and quantitative defenses, the former will increase and the latter will decrease in response to stress, presumably due to the cost differences between the two modes of defense. Bracken fern (*Pteridium aquilinum*) contains cyanogenic glycosides (qualitative) and tannins (quantitative) and their concentrations follow the proposed scheme in response to shade (Cooper-Driver et al. 1977).

Response of Goats to Blackbrush Manipulation

Comparison of does and kids

A critical way in which ruminants interact with their environment is through the process of grazing. Many animal-, plant-, and environment-related factors interact to determine the food items selected by an herbivore (Figure 2), and the composition of the diet will usually be different than the proportions of the various plant species and parts available. Selection for a particular plant species or part, which is a behavioral response by the grazing animal (Heady 1964), is determined by genetics, by the animals' prevailing nutritional and physiological state, and by previous experience (Malechek and Provenza 1981). Selection is relative and depends on the array of choices available.

Evolution, acting through natural selection, should favor those animals (genotypes) best able to meet their nutritional requirements. Domesticated animals, however, have been selectively bred for hair, meat, and milk production, and now graze rangelands where they did not evolve. In this light, the assumption that animals should graze to optimize nutrient (Westoby 1974) or energy (Emlen 1966) intake may be unreasonable. The fact that species such as goats have persisted and flourished, however, indicates that their sensory responses still result in adequate nutrition, and that diet selection is probably the outcome of innate behavior plus learning as a result of experiences in early and adult life (Arnold and Dudzinski 1978, McClymont 1967).

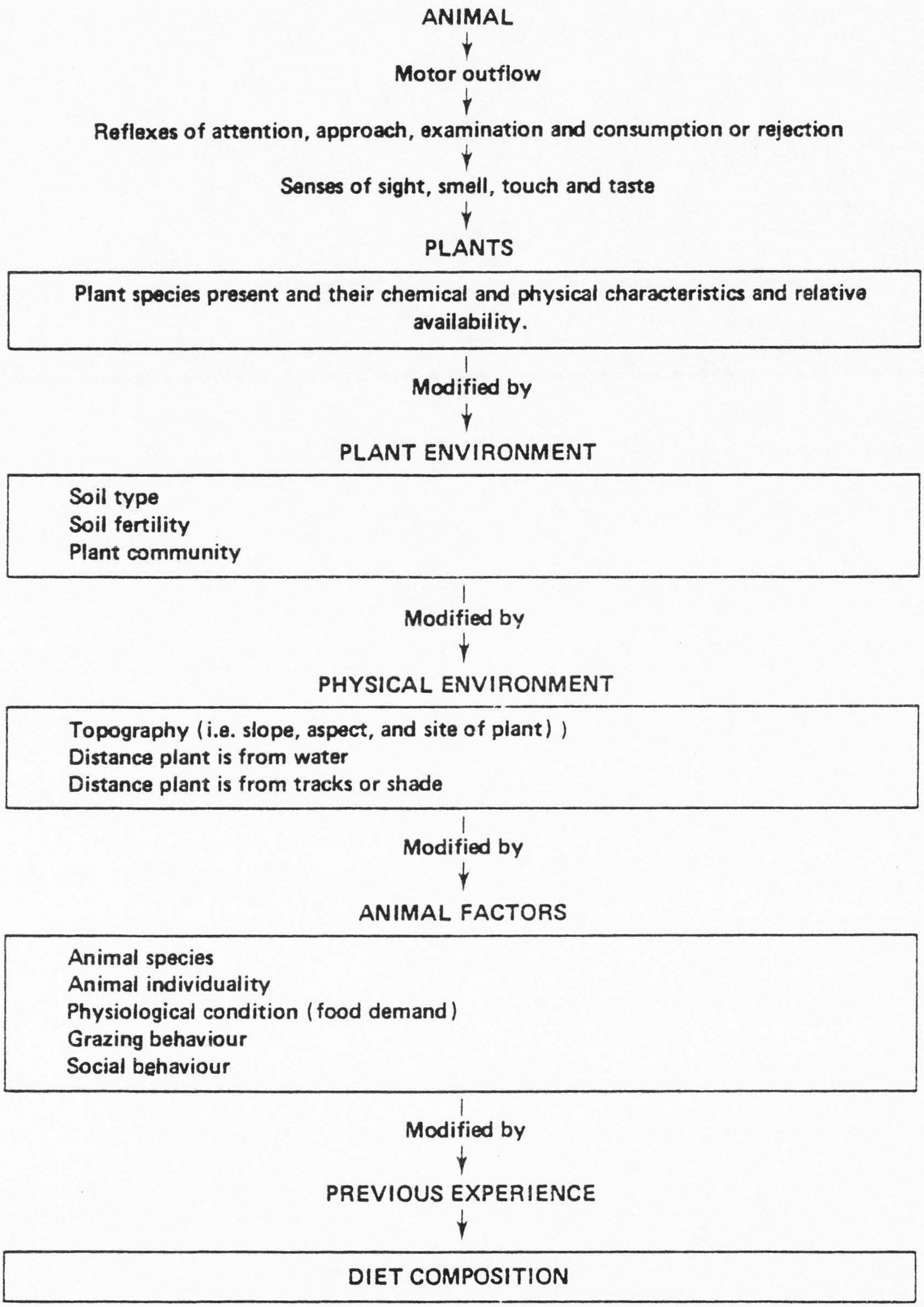


Figure 2. Various factors influencing diet composition. From Arnold and Dudzinski (1978).

The previous experiences of adult and juvenile goats differed because does had previously browsed blackbrush plants, while kids were raised from birth on alfalfa hay. Arnold and Maller (1977) showed that sheep raised on hay from birth until 3 years of age grazed 20 percent longer but consumed 40 percent less food than sheep reared on phalaris pastures. The time and energy animals expend foraging are substantial (Malechek and Smith 1976, Osuji 1974), therefore an adaptive advantage is gained by the animal minimizing grazing time while maximizing nutrient and energy intake.

Adult and juvenile goats also have different nutritional requirements. Huston et al. (1971) recommended that Angora does consume a diet containing 2.2 $mcal \cdot kg^{-1}$ of digestible energy and 9.0 percent crude protein during early pregnancy and 2.4 $mcal \cdot kg^{-1}$ of digestible energy and 10.0 percent crude protein during the last eight weeks of pregnancy. Recommended requirements for kids were 2.9 $mcal \cdot kg^{-1}$ of digestible energy and 11.6 percent crude protein. Requirements of Spanish goats may be lower since they produce less hair, but the relative differences between does and kids should remain. Arnold and Dudzinski (1978) discussed nutritional data from Arnold, Campbell, and Pahl (unpublished) for sheep of different ages and indicated that sheep aged five months consumed a diet that was higher in nitrogen content and more digestible than that of older sheep. The differences may have been due to increased selection by the lambs or to their smaller jaw.

The senses of sight, touch, taste, and smell are involved in diet selection and numerous attempts have been made to relate plant characteristics and preference (Arnold and Dudzinski 1978). Where causative correlations are found they must relate to specific compounds within the plant or some physical property of the plant. Acceptance or rejection is probably the result of an integrated response by the animal to more than one plant characteristic (Arnold and Dudzinski 1978) and significant animal-to-animal variation in selective response is common (Arnold et al. 1980, Arnold 1964). As Arnold and Hill (1972) pointed out, the senses of taste and smell operate at the molecular level and animals have no means of recognizing such complexes as crude protein and energy.

Tannins have been shown to decrease the palatability and digestibility of forages. Arnold et al. (1980) indicated that sheep initially rejected, but later habituated to, the odor of tannic acid and that the taste of solutions as low as 0.05 percent tannic acid were rejected. Tannic acid also reduced in vitro dry-matter digestibility and dry-matter intake, but these researchers believed that reduced intake was the result of reduced microbial activity in the rumen, since asensory and normal sheep showed similar decreases in intake. Wilkins et al. (1953) demonstrated a 73 percent decrease in voluntary intake of Sericea lespedeza by cattle as tannin levels increased from 4.8 to 12.0 percent, and tannins were shown to inhibit cellulose digestion (Lyford et al. 1967, Smart et al. 1961).

The occurrence of high tannin concentrations within plants undoubtedly affects palatability, but other plant characteristics also interact to increase or decrease acceptability to herbivores. For example, Donnelly (1954) found the palatability of Sericea lespedeza was related to stem diameter and pliability, as well as tannin levels; the most palatable plants had small, pliable stems which contained low tannin levels.

Supplementation

Provenza (1977) indicated that goats browsing blackbrush pastures lost weight and that weight loss may have been due to low protein levels. Protein is one of the most important nutrients to ruminants because of its profound effect on energy relationships specifically, and on metabolic processes in general. Microbial protein, which is of consistently high biological value (Bergen et al. 1967, McNaught et al. 1954, Johnson et al. 1944), comprises the major portion of the ruminants nitrogenous food (Hungate 1966). Therefore, a decrease in microbial cell production results in a decrease in digestible protein for the ruminant.

Most of the energy available to ruminants results from microbial breakdown of soluble and insoluble carbohydrates. The most important end products of these fermentations are the volatile fatty acids such as acetic, propionic, butyric, valeric, and isovaleric. These volatile fatty acids are absorbed through the rumen wall and supply approximately 50 to 70 percent of the energy requirement of the ruminant (Annison and Lewis 1959).

When ruminants consume high-fiber diets, fermentation in the rumen is regulated primarily by the cellulolytic bacteria, and secondarily by the amylolytic and saccharolytic bacteria (Schwartz and Gilchrist 1975). The cellulolytic bacteria require ammonia for growth (Bryant and Robinson 1961), while growth of the amylolytic and saccharolytic bacteria is stimulated by organic sources of nitrogen such as amino acids (Maeng and Baldwin 1976). The primary result of low dietary protein levels is decreased microbial cell production which causes decreased cellulose and hemicellulose digestion (van Glyswyk 1970, Jones et al. 1970, Moir and Harris 1962). As a result, daily food intake decreases, impairing the ruminant's ability to meet daily energy requirements. Decreased microbial cell yields also reduce the amount of digestible protein, in the form of microbes, available to the ruminant. The consequence of less digestible protein and energy is a weight loss by the animal.

Van Gylswyk (1970) studied the effects of supplementing low-protein hay with urea, urea plus volatile fatty acids, and protein (egg albumin) on sheep (Table 1). His results illustrate the effects of supplementing protein and energy on rumen microorganisms and the ruminant. The low nitrogen content of the hay resulted in low numbers of ruminal bacteria attacking cellulose and hemicellulose, which prevented the sheep from digesting enough hay to meet their daily energy requirements. Addition of urea to the diet increased bacterial proliferation in the rumen which increased the digestion of cellulose and hemicellulose and allowed the animals to increase daily intake by 185 gms. The concentration of cellulolytic bacteria in the rumen did not increase, however, due to an increased rate of passage of ingesta through the rumen (Gilchrist and Kistner 1962).

With the nitrogen deficit rectified, the next factor limiting hay utilization was lack of volatile fatty acids. Volatile fatty acids are required for the growth of several species of cellulolytic

Table 1. Effects of various supplements on sheep fed a poor quality hay diet. Data from van Gylswyk (1970).

Supplement	Percent Crude Protein	Mean Daily Intake (g)[1]	Cellulolytic Bacteria Counts (g^{-1} rumen fluid)	Percent Digestibility[2]		Energy[2, 3] ($therms \cdot day^{-1}$)		Percent Weight Change[1]
				Cellulose	Hemicellulose	Required	Obtained	
None	3.3	717	4.0×10^7	57	45	2.3	0.7	-19.0
Urea	10.4	902	4.0×10^7	72	64	2.7	2.2	- 8.2
Urea/VFA[4]	11.2	1077	9.8×10^7	72	67	2.9	2.6	- 3.8
Egg albumin	9.9	1086	2.7×10^7	65	63	2.5	2.8	+ 4.7

1/ Averaged over a 12-week trial.

2/ Averaged over the last 2 weeks of a 12-week trial.

3/ Assumed 0.058 therms required $\cdot$ kg^{-1} of body weight. Average sheep weights at the initiation of the trial were 39.3, 46.2, 50.0, and 43.0 kg for the none, urea, urea/VFA, and egg albumin treatments, respectively.

4/ VFA represents volatile fatty acids.

bacteria, and are usually derived from protein in the diet (Allison 1965, Bryant and Robinson 1962, 1963, Allison et al. 1958). Addition of volatile fatty acids to the diet increased the proliferation rate of cellulolytic bacteria in the rumen, allowing the supplemented sheep to increase hay intake to nearly twice that of the unsupplemented sheep. This supplement failed, however, to supply the energy necessary for maintenance. Van Glyswyk (1970) indicated that this failure may have resulted from the limited quantity of hay offered to the sheep, since they consumed their entire ration. He suggested that since the concentration of cellulolytic bacteria in the rumen ingesta for this diet was twice that of the previous two diets, sufficient numbers of microorganisms were present to digest more hay. These results support the findings that urea, or other forms of nonprotein nitrogen, are less effective supplements for poor quality roughages than are plant or animal proteins, since such proteins provide both nitrogen and precursors of the branched-chain volatile fatty acids.

Supplementation of hay with egg albumin resulted in decreased numbers of cellulolytic microorganisms in the bacterial population. This was probably due to competition with other species which benefited from the egg protein. The decline in the number of cellulolytic bacteria was associated with a slight decrease in the digestibility of cellulose and hemicellulose. However, the egg albumin provided sufficient energy for weight gains during the trial.

The affinity of tannins for proteins results in an inverse relationship between tannin content and protein digestibility

(Donnelly and Hawkins 1955, referenced by McLeod 1974). Tagari et al. (1965) indicated that proteolytic activity and protein biosynthesis were significantly depressed by tannins. Lyford et al. (1967) found that tannin extracts from *Sericea lespedeza* inhibited the cellulolytic enzyme system in the rumen, but that added protein prevented the inhibition. Horvath et al. (1980) obtained improved in vitro cell wall digestibilities by the addition of soybean protein to tannic acid.

Tannins and lignins play a similar role in the plant by binding proteins and carbohydrates (Swain 1979), and care must be exercised to differentiate between the effects of tannins and lignins on digestibility. Though *Lespedeza cuneata* is high in tannins, Hawkins (1955) suggested that the low dry matter digestibility was due to high lignin content, as well as low protein digestibility due to tannins. Burns et al. (1972) found that heifers adapted to increased tannin levels more readily than to increased fiber levels, and Van Soest and McCammon-Feldman (1980) suggested that microbial adaptation to tannins may occur.

Response of Cattle to Blackbrush Manipulation by Goats

Comparison of goat-browsed and unbrowsed pastures

Published research on the use of goats to improve rangelands for cattle is limited. Most research has been directed toward control of undesirable species, rather than alteration of plant morphology. Domestic goats have been used successfully as biological controllers of oak woodlands in Texas (King 1956, Magee 1957, Norris 1968) and Colorado (Davis et al. 1975), and of Acacia-dominated ranges in South Africa (De Toit 1973).

The potential of the goat for common use of rangelands with cattle can be viewed from several aspects. Firstly, land managers are interested in biological techniques for manipulating vegetation. With mounting concerns for environmental protection and energy costs, traditional range improvement tools such as chemical herbicides, chaining, plowing, and burning are receiving close scrutiny. Controlled browsing, however, can often accomplish comparable goals with fewer environmental risks.

Secondly, some authorities (Martin 1970, Box 1974) believe that for rangelands to contribute fully toward supplying mankind's future needs for animal protein, unconventional kinds of animals will be needed. The shrub component of rangelands represents a food niche that is often underutilized by our present mix of domestic animals. The goat is a strong candidate for filling this niche in many areas, but the specifics for managing the animal are poorly understood.

Finally, with encroachment by an expanding human population, common use of rangelands by animal species whose food habits are complementary will be increasingly important. With its preference for woody vegetation, the goat has the potential for complementing species such as cattle that prefer herbaceous vegetation (Wilson 1969).

Researchers (Sampson and Jespersen 1963, Humphrey 1953, 1955) indicated that blackbrush was better forage for goats than for cattle. Goat browsing may result in blackbrush plants which are less spinescent, and have more available forage of higher nutrient content and digestibility, than unbrowsed plants (Provenza 1977). As a result, goat-browsed shrubs may be more acceptable to cattle.

The potential exists for common use of blackbrush rangelands by goats and cattle. While a large market does not currently exist for mohair or meat in southern Utah, a market is developing in southern California. In the future, common use of blackbrush rangelands by goats and cattle may be economically feasible.

STUDY AREA

The experiment was conducted on Bureau of Land Management administered land in the extreme southwestern corner of Utah near the town of Gunlock, located at 37.5^{o} north latitude and 114^{o} west longitude. The site was within the area studied by Bowns (1973) and Bowns and West (1976) in their autecological investigations of blackbrush and was considered representative of the blackbrush type. The reader is referred to these publications for a detailed description of vegetation, soils, and climate of the area.

The study area (Figure 3) was at an elevation of 1280 m and consisted floristically of blackbrush associated with juniper (*Juniperus osteosperma*). The soil series of the site as a Pastura Loam with an A-C horizon sequence underlaid by a petrocalcic (caliche) horizon (Bowns 1973). A Bureau of Land Management rain gauge at Tobin Wash, located approximately 2 km west of the study site, showed an annual average of 276 mm of precipitation during the period October 1965 to October 1976. An annual average of 361 mm of precipitation was recorded during the study, October 1976 to October 1980.

The physical design of the experiment consisted of two blocks of 8 ha each (Figure 4). Within each block the control and heavily stocked pastures were 1 ha, the moderately stocked pasture was 2 ha, and the lightly stocked pasture was 4 ha. These areas were enclosed by a 1.2 m net wire fence supported by steel posts.

Figure 3. The study site illustrating the juniper overstory and blackbrush understory.

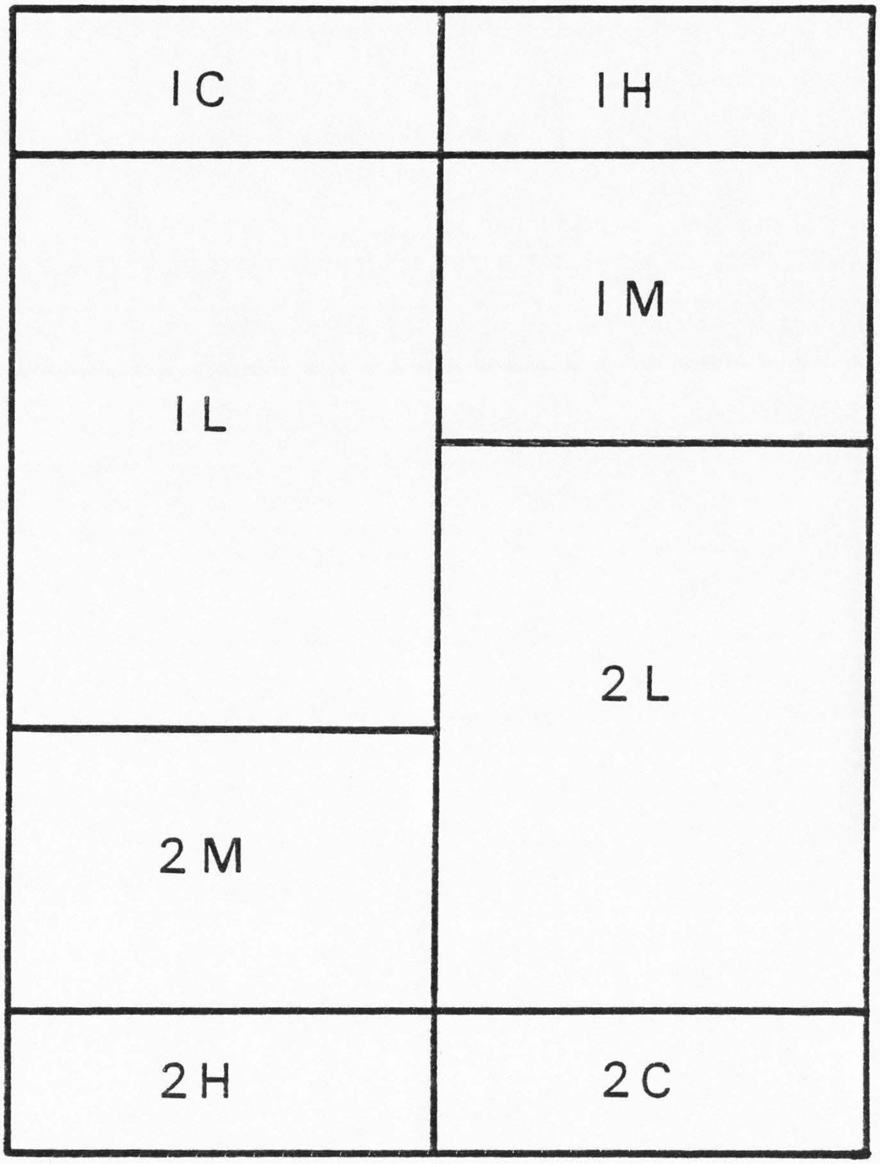


Figure 4. Pasture layout for the blackbrush study site. A prefix of 1 or 2 indicates the replicate, and a suffix of H, M, L, or C indicates a stocking intensity of heavy, moderate, light, or control, respectively.

The statistical design of the experiment was a factorial arranged in randomized blocks. There were four rates of stocking and the experiment was replicated twice. For determining pasture utilization and production, a sampling intensity of 50 plants per hectare was employed in a restricted random sample. Five transects were systematically established in each of the 1 and 2 ha pastures. Ten plants were randomly selected along each transect in the 1 ha pastures, and 20 plants were randomly selected along each transect in the 2 ha pastures. Ten transects were systematically established in each of the 4 ha pastures, and 20 plants were randomly selected along each transect.

METHODS

Response of Blackbrush to Goat Browsing

Morphological

Stocking intensities and utilization levels. Due to the low utilization levels recorded by Provenza (1977), the length of the browsing periods for this study were increased. The objective was to obtain maximum utilization before mid-March when blackbrush generally begins growth (Bowns 1973). The browsing periods employed in this study are summarized in Table 2, and the resultant stocking intensities are presented in Table 3.

Utilization was determined by the method of Provenza and Urness (1981) in which caliper measurements of branch diameters were used to predict the length of twig material present before and after browsing. A branch was that portion of the plant arising from the ground, and twigs were subdivisions of the branch. Prior to the browsing period, a point on each sample branch was marked with red ink and a caliper measurement made at that point to predict twig material originally available. After the browsing period, each browsed tip distal to the marked point was measured to predict the amount of twig material removed. The regression equation used to predict twig lengths from branch diameters was:

$$\text{natural logarithm length} = 4.0398 + 2.3855\ (\text{natural logarithm diameter})$$

Table 2. Browsing periods for the blackbrush study.

Class of Animal	Year	Browsing Period
Goat[1/]	1977	9 January - 10 March
Goat	1978	29 December - 11 March
Goat	1979	2 January - 17 March
Cattle	1979	1 October - 28 October

1/ Data from Provenza (1977).

Table 3. Stocking intensities for the blackbrush study.

Pasture	Stocking Intensities[1/]			
	1977[2/] (goat)	1978 (goat)	1979 (goat)	1979 (cattle)
Control	0	0	0	2.3
Light	0.3	0.6	0.5	0.6
Moderate	0.6	1.2	1.0	1.1
Heavy	1.2	2.4	2.0	2.3

1/ Animal-unit-months·hectare^{-1}; animal units for goats and heifers were computed on a weight basis with a 454 kg cow equal to one animal unit.

2/ Data from Provenza (1977).

Percent utilization was computed as follows:

$$U = \frac{\Sigma PB}{PT} (100)$$

where U = percent utilization

ΣPB = sum of the predicted browsed branch lengths

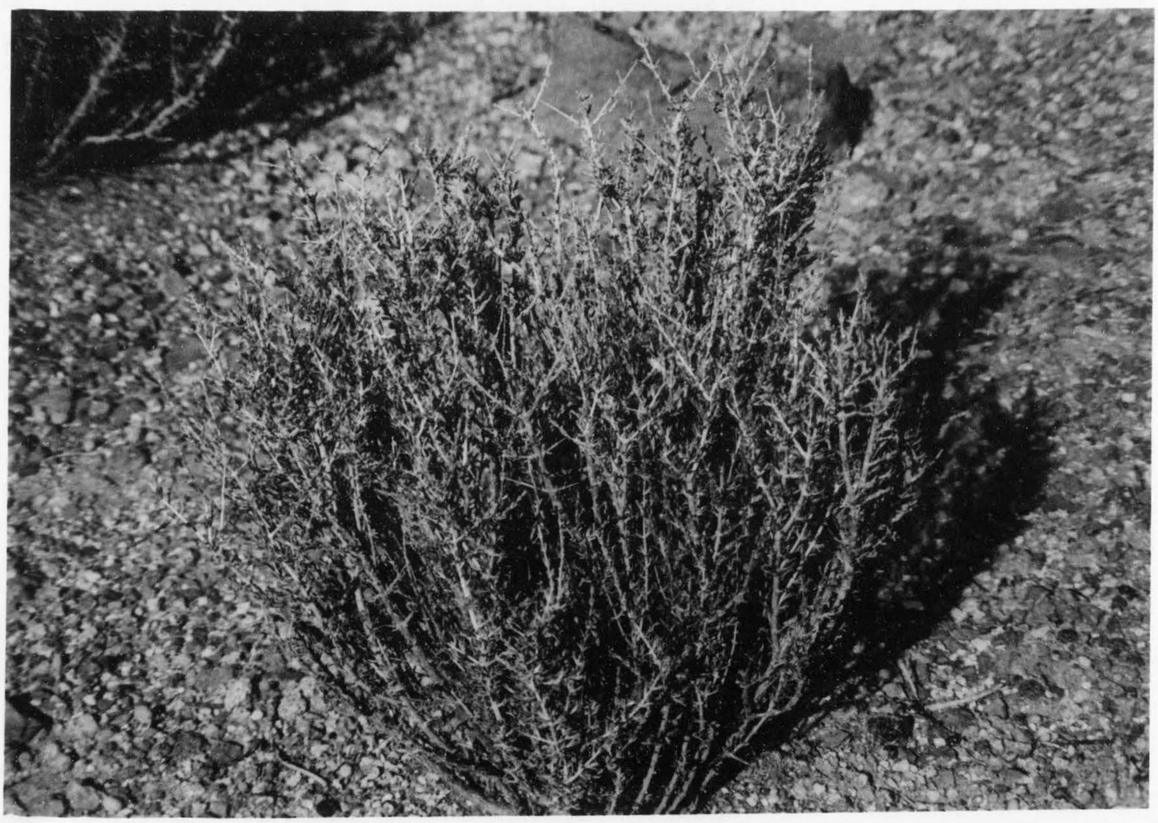
PT = predicted branch length before browsing

Percent utilization was measured on two branches from each sample plant. A terminal branch was selected from older branches growing on the outer edges of the plant, and a basal branch was selected from sprouts and young branches arising from within the terminal branch canopy (Figure 5).

Twig growth. Total length of seasonal twig growth on a terminal and basal branch from each sample plant was measured in September after blackbrush growth ceased (Bowns 1973). Random selection of both branches was assured by placing a circular hoop 0.9 m in diameter and covered with a 5 cm wire grid over each plant. The grid was supported by a metal stake which allowed the grid to revolve. The stake was positioned in the center of each sample plant, and the grid was spun and allowed to come to rest. A metal pin was inserted at pre-determined points on the grid intersections, and the current season's growth on the terminal or basal branch nearest a pin was measured to the nearest 1 mm.

Factors affecting twig growth. To assess the effects of soil depth and stoniness on production of current season's twigs, 36 plants were selected on both deep and shallow soils. The average depth to the impervious caliche layer for deep and shallow soils was 71 and

Figure 5. An extremely spinescent (top) and less spinescent (bottom) blackbrush plant. Terminal branches are older branches growing on the outer edges of the plants. Basal branches are sprouts and young branches arising within the terminal branch canopy, and as a result are not visible.



39 cm, respectively, and shallow soils contained surface and subsurface stones.

Within each soil depth, the effects of heavy use followed by rest were investigated (Table 4). Heavy use in the initial year (1977) was removal of twigs from all of the terminal branches. Subsequently, heavy use was greater than 95 percent removal of current season's twigs from terminal and basal branches.

Three terminal and three basal branches were randomly selected and measured on all plants except control. One terminal and one basal branch was measured on control plants in 1977, 1978, and 1979. Branches were measured in Decemher of 1977 and September of 1978, 1979, and 1980 according to the procedure described in the section entitled "Twig growth". The statistical design of the experiment was a factorial with repeated measurements on the plants. Soil depth and "years" were the main effects, and branch location within plants was treated as a subplot in the analysis.

Chemical

Nutritional properties of twigs. Hand-plucked blackbrush samples that simulated twigs consumed by goats browsing current season's and older growth from the terminal branches of plants growing on deep and shallow soils were analyzed for crude protein, phosphorus, and in vitro dry-matter digestibility. Eight plants were sampled within each treatment (current season's versus older growth) by soil depth (deep versus shallow) combination, and samples were collected in January of 1978 and March of 1979. The statistical

Table 4. Years in which blackbrush plants growing on deep and shallow soils were browsed and rested from browsing.

Treatment Symbol ("years")	Number of Plants	Year	
		Browsed	Rested
B0 R4	6	--	1977, 1978, 1979, 1980
B1 R3	6	1977	1978, 1979, 1980
B2 R2	6	1977, 1978	1979, 1980
B3 R1	6	1977, 1978 1979	1980
B4 R0	6	1977, 1978, 1979, 1980	--
B1 R0	6	1980	--

design for this experiment was a factorial with plant type, soil depth, and year as the main effects and the experiment was replicated twice (1978, 1979).

Prior to chemical analysis, samples were air-dried and ground through a Wiley mill with a 40-mesh·cm^{-1} screen. Samples were analyzed in duplicate, and results were expressed on a dry-matter basis. Crude protein content was determined by the Kjeldahl method (Horwitz 1970), phosphorus content was determined by the ammonium molybdate-ammonium vanadate method described by Chapman and Pratt (1961), and in vitro dry-matter digestibility was determined by the two-stage method described by Tilley and Terry (1963). Rumen inocula were obtained by sacrificing a goat which had been browsing blackbrush pastures in 1978, and by stomach pump from three esophageally fistulated goats fed alfalfa hay in 1979.

In an additional study, hand-plucked blackbrush samples that simulated twigs consumed by goats browsing current season's terminal versus basal branches were analyzed for crude protein and in vitro dry-matter digestibility. The terminal and basal branches from six plants were collected during March of 1979 and analyzed as described above. The statistical design for this study was a factorial with six replications (plants) of two treatments (terminal and basal).

Anti-nutritional properties of twigs. To assess the effects of soil depth, heavy browsing followed by rest, and branch location on the tannin content of blackbrush twigs in 1980, the terminal and basal branches from three plants in each treatment combination in Table 4 were clipped, air-dried, and ground through a Wiley mill with a 40-mesh$\cdot$cm^{-1} screen. Samples (200 mg) were analyzed in duplicate, and results were expressed on a dry-matter basis. The statistical design of this experiment was a factorial with soil depth and "years" as main effects. The plant effect was nested within these effects, and branch location within plants was treated as a subplot in the analysis.

To determine the relative contribution of leaves and stems to tannin levels in current season's twigs growing on terminal and basal branches, samples from six blackbrush plants were analyzed. Leaves and stems were analyzed separately for tannin content. The statistical design for this analysis was a factorial with plant part (leaves and stems) and branch location (terminal and basal) as the main effects. The experiment was replicted (plants) six times.

Various methods of analysis are available for detecting tannins in plant material, but preferred methods of analysis are based on the ability of tannins to form complexes with protein, since this provides a measure of the biologically active tannins in the sample (Swain 1979, McLeod 1974). The method used in this study involved adding crude methanolic extracts of plant tannins to a standard protein solution (Hagerman and Butler 1978). The tannin-protein complex which formed was a relative measure of the biologically active tannins in the sample, and this was measured spectrophotometrically at 510 nm.

Response of Goats to Blackbrush Manipulation

Comparison of does and kids

Six does, with previous experience browsing blackbrush plants, and six nine-month-old kids, raised on alfalfa hay, browsed in both a heavily (2.0 $AUM \cdot ha^{-1}$) and a lightly (0.5 $AUM \cdot ha^{-1}$) stocked blackbrush pasture from January until mid-March of 1979 (Table 2). Three of the does and three of the kids in each pasture were fitted with esophageal fistulae two months prior to the experiment. Data relative to diet samples and activity budgets were collected from these goats.

Diets. Fistulae extrusa samples were collected 11 times during the browsing period. The goats were originally penned overnight prior to early morning collections (8 a.m.). This did not correspond with an active feeding time (10 or 11 a.m.), however, and the goats were subsequently penned at 8 a.m., with access to water, and collections made around noon. The animals were allowed to browse for 30 to 45 minutes with their fistulae plugs removed and collection bags attached. Fistulae extrusa samples were hand mixed, placed in plastic bags, and frozen. Prior to botanical and chemical analysis, the samples were freeze dried.

The point-intercept technique of Chamrad and Box (1964) was used for the botanical analysis. Samples were separated into the following categories: (1) blackbrush leaves and stems, (2) dry grasses and forbs, (3) green grasses and forbs, (4) alfalfa, (5) desert peachbrush (*Prunus fasciculata*), (6) pinyon (*Pinus* monophylla, and (7) juniper (Juniperus osteosperma). The ratio of blackbrush leaves to stems, based on hits, was converted to a weight ratio by a regression equation established using the point-intercept technique on artificial diets of known leaf and stem weights. For the chemical analysis, the samples were ground through a 40-mesh·cm^{-1} screen and analyzed, as previously described, for crude protein, in vitro dry-matter digestibility, and tannins. The statistical design for the botanical and chemical analyses was a factorial with repeated measurements. Stocking rate and age class were the main effects with the goat effect nested, and the experiment was repeated on 11 dates during the browsing period.

Preliminary analysis of esophageal fistula extrusa for tannins indicated markedly lower levels than generally available in the blackbrush plants on offer. This suggested two possibilities: (1) goats selected to an extreme degree against tannin-containing twigs, and/or (2) the process of mastication reduced the amount of biologically active tannins in the sample.

To assess the degree to which mastication reduced detectable tannins in blackbrush, four esophageally fistulated goats were fed terminal and basal branches. For each goat, a sample of each branch type was clipped and divided into two parts. Half of each sample was fed and subsequently retrieved from the collection bag, while the other half was saved for analysis on an as-clipped basis. All samples were frozen for transportation to the lab where they were freeze dried prior to analysis. The freeze dried twigs were ground through a Wiley mill with a 40-mesh·cm^{-1} screen prior to analysis of duplicate, 200 mg samples. The statistical design for this experiment was a factorial with repeated measurements on the goats. Mastication and branch location were the main effects, and the animal effect was nested within the mastication effect.

Activity budgets. Foraging, by virture of high energy cost and large quantity of time invested in the activity, represents a major energy expenditure for rangeland animals (Malechek and Smith 1976). Since the energy cost of foraging is directly related to the time spent foraging (Osuji 1974), the time goats in blackbrush pastures spent browsing was an indirect measure of energy expenditure.

Scan samples (Altmann 1974), at 10-minute intervals from 8 a.m. to 5 p.m., were used to determine the amount of time does and kids spent browsing. Lightly and heavily stocked pastures were sampled on successive days during the browsing season. The statistical design for this experiment was a factorial with repeated measurements. The main effects were stocking rate, age class, and fistulation (fistulated and nonfistulated), and the animal effect was nested within the main effects. The experiment was repeated 11 times during the browsing period.

Weights. To supplement diet sample and activity budget data, the animals were weighed five times during the browsing period. Goats were penned overnight without access to feed or water prior to weighing. Two statistical analyses were performed on the data. The first design was a factorial involving the heavy and light pastures. Stocking rate (heavy versus light), age class (does versus kids), and fistulation (fistulated versus nonfistulated) were the main effects with the goat effect nested, and the experiment was repeated five times. The second design was a split-split plot involving all the pastures. The whole plot effect was stocking rate, the sub-plot effect was age class, and the sub-sub-plot effect was date.

Supplementation

Requirements. Provenza (1977) indicated that Angora goats browsing blackbrush rangelands lost weight and recommended supplementation with protein and energy. During the winter of 1978, Spanish goats browsing blackbrush pastures were supplemented with a 50 percent corn-50 percent soybean ration. The recommended requirements for Angora goats (Huston et al. 1971), and the approximate amount of protein and energy provided by the supplemental ration, are shown in Table 5. The energy requirement listed by Huston et al. (1971) is somewhat higher than tabled values for feedlot (e.g., Church 1979), primarily because Huston et al. (1971) attempted to account for the additional energy requirements associated with foraging.

Prior to the initiation of the study, half of the goats to be placed in each pasture were randomly selected to be supplemented. From January 5 to February 17, goats were group fed the equivalent of 0.82 kg of supplement per animal every-other-day. Due to overeating and the large amount of readily fermented carbohydrates in the ration, some goats suffered acute indigestion. As a result, from February 20 to March 11, the supplemented group received the equivalent of 0.45 kg per individual every-other-day.

Table 5. Amount of protein and energy provided by two levels of a 50 percent corn-50 percent soybean supplement relative to daily Angora goat requirement.

Item	Dry Matter (kg)	Digestible Protein (kg)	Digestible Energy (mcal)
Requirement[1/]	1.8-2.0	0.11-0.12	4.5-4.7
0.82 kg supplement[2/]	0.7	0.16	6.2
0.45 kg supplement[3/]	0.4	0.10	3.5

[1/] Recommended daily intake for a 36 kg Angora doe during the last eight weeks of pregnancy (Huston et al. 1971).

[2/] Quantity of supplement received by goats on an every-other-day basis from January 5 to February 17 of 1978.

[3/] Quantity of supplement received by goats on an every-other-day basis from February 20 to March 11 of 1978.

Weights. Goats were weighed, after being penned overnight without access to feed or water, at two week intervals during the browsing period. The statistical design for the weight response data was a split-split-plot with two replications. Stocking rate was the whole plot effect, supplementation was the sub-plot effect, the date was the sub-sub-plot effect.

Response of Cattle to Blackbrush Manipulation by Goats

Comparison of goat-browsed and unbrowsed pastures

Thirty-two Hereford cattle (yearling heifers) browsed blackbrush pastures from October 1 to October 28 of 1980. These heifers were placed in a blackbrush holding pasture during the last week in September. On October 1 they were weighed, and four animals were randomly assigned to each of the eight blackbrush pastures (Figure 4). Six of these pastures had been browsed previously by goats, while two of these pastures were previously unbrowsed (Table 3). Diet sample, activity budget, and weight response data were collected at two week intervals during the browsing period.

Diets. Hand-plucked blackbrush samples that duplicated twigs consumed by cattle were collected, after two and four weeks of browsing, from animals in the four pastures of replication one (Table 6). Within a pasture, each animal was observed during the day and the blackbrush plants and plant parts being consumed were sampled.

Table 6. Dates on which diet sample and activity budget data were collected from heifers browsing in replication one.

	Date in October							
	Two Weeks				Four Weeks			
	9	10	11	12	23	24	25	26
Diet samples	L[1/]	M	H	C	L	M	H	C
Activity budgets	L	M	H	C	L	M	H	C

[1/] L, M, H, and C refer to light, moderate, heavy, and control pastures, respectively.

Samples were separated into current season's versus older growth and weighed for the botanical analysis. For the chemical analysis, current season's and older twigs were pooled, ground through a Wiley mill with a 40-mesh$\cdot$cm^{-1} screen, and analyzed for crude protein, in vitro dry-matter digestibility, and tannins as described in a previous section entitled "Response of Goats to Blackbrush Manipulation". The statistical design for this experiment was a factorial with repeated measurements. The main effect was stocking rate, and animals were nested within this effect. The experiment was repeated twice during the browsing period.

Activity budgets. The amount of time cattle in blackbrush pastures spent browsing was used as a relative indication of energy expenditure (Malechek and Smith 1976, Osuji 1974). Scan samples (Altmann 1974), at 10-minute intervals from 8 a.m. to 7 p.m., were used to determine the amount of time heifers in replication one spent browsing (Table 6). The statistical design for this experiment was a factorial with repeated measurements. The main effect was stocking rate, and animals were nested within this effect. The experiment was repeated twice during the browsing period.

Weights. Heifers in all blackbrush pastures had access to 36 percent protein-block supplement during the browsing period. Block consumption was recorded by pasture on a weekly basis. The animals were weighed after two and four weeks of browsing, having been penned overnight without access to feed or water prior to weighing. The statistical design for these studies was a split plot with two replications. The whole plot effect was pastures, and the sub-plot effect was dates.

RESULTS AND DISCUSSION

Response of Blackbrush to Goat Browsing

Morphological

Stocking intensities and utilization levels. Table 7 summarizes stocking intensities and utilization levels for blackbrush pastures during this study, and the analyses of variance are presented in Appendix Tables 15-17. The data in Table 7 not only established stocking intensities and utilization levels for goats and cattle, but also indicate how the animals utilized blackbrush. At similar stocking intensities, blackbrush utilization by goats (1978) and cattle (1979) was comparable. Basal and terminal branches were used by both goats and cattle with a trend toward greater use of basal branches. This is particularly interesting with respect to cattle since their large muzzle would appear to make access to basal branches more difficult than for goats. As utilization levels increased, however, cattle were apparently unable to consume basal branches as completely as goats (e.g., 1978 goat versus 1979 cattle utilization), probably due to their large muzzle. Due to the small size of blackbrush leaves, goats and cattle were unable to select to any great degree for leaves; rather, they consumed leaves with the twigs and leaf stripping was not practiced.

Also of importance was the goats' aversion to current season's growth (CSG) on terminal branches, particularly in 1979. Increased

Table 7. Stocking intensities and utilization levels for blackbrush pastures.

Pasture	1977 (Goat)[1/]		1978 (Goat)				1979 (Goat)				1979 (Cattle)			
	Stocking Intensity[2/]	Percent Utilization Terminal	Stocking Intensity	Percent Utilization			Stocking Intensity	Percent Utilization			Stocking Intensity	Percent Utilization		
				Terminal[3/]	Basal	Average		Terminal	Basal	Average		Terminal	Basal	Average
Control	0	0	0	0	0	0	0	0	0	0	2.3	82	77	80^{a}
Heavy	1.2	33^{a}	2.4	72	82	77^{a}	2.0	39^{d}	67^{e}	53^{a}	2.3	83	74	79^{a}
Moderate	0.6	18^{ab}	1.2	39	49	44^{b}	1.0	29^{d}	30^{d}	29^{ab}	1.1	47	52	49^{b}
Light	0.3	6^{a}	0.6	20	24	22^{c}	0.5	11^{d}	14^{d}	12^{b}	0.6	22	33	27^{c}

1/ Data from Provenza (1977).

2/ Animal-unit-months·hectare^{-1}; animal units for goats and heifers were computed on a weight basis with a 454 kg cow equal to one animal unit.

3/ Terminal versus basal branches in 1978 (P=0.10).

abc Means in the same column followed by a different letter are significantly different ($P<0.05$).

de Mean in the same row followed by a different letter are significantly different (P=0.03).

utilization levels and ample moisture stimulated spring twig production in 1978. As a result, the terminal and basal twigs available for goats browsing in the heavily stocked pasture in 1979 consisted entirely of CSG. Goats browsing in the heavily stocked pastures during 1979, however, ate relatively little CSG from terminal branches, and nonsystematic observations indicated that terminal branch consumption increased only after basal branch availability was greatly reduced.

Table 8 is a summary of data presented in Table 7 intended to show aggregate grazing capacities for cattle and goats during 1979. Stocking intensities of 4.3 and 2.1 animal-unit-months$\cdot$ha^{-1} for the heavy and moderate treatments, respectively, were achieved during a single year from two forage crops (1978, 1979) without evident overuse of the shrub resource. This is remarkable, considering conventionally-held beliefs that blackbrush ranges have inherently low grazing capacity. Even the 2.3 animal-unit-month$\cdot$ha^{-1} stocking intensity on previously unbrowsed (control) pastures was 29 times higher than agency guidelines of 0.08 animal-unit-months$\cdot$ha^{-1} (Jenson et al. 1960).

One major consideration in this argument is whether blackbrush plants could withstand, over the long term, heavy winter use by goats followed by heavy fall use by cattle. However, results presented later show that plant vigor was not lowered by four consecutive years of extremely heavy utilization.

Twig growth. Differences in production of CSG resulting from goat browsing at various stocking intensities were not highly

Table 8. Cumulative blackbrush use by goats (2 January to 17 March) and cattle (1 October to 28 October) during 1979.

Pasture	Goat		Cattle		Goat and Cattle
	Stocking Intensity[1/]	Percent Utilization	Stocking Intensity[1/]	Percent Utilization	Stocking Intensity[1/]
Control	0	0	2.3	80	2.3
Heavy	2.0	53	2.3	79	4.3
Moderate	1.0	29	1.1	49	2.1
Light	0.5	12	0.6	27	1.1

1/ Animal-unit-months · $hectare^{-1}$; animal units for goats and heifers were computed on a weight basis with a 454 kg cow equal to one animal unit.

significant (Appendix Tables 18-19), however, trends were apparent (Table 9). Heavy stocking intensities resulted in the greatest twig production. The lack of statistical significance among moderate, light, and control pastures resulted from variable goat use of individual plants in the lightly and moderately stocked pastures. This caused individual plant production to vary greatly within treatments, and resulted in significant error variation. The differences in plant production among years were due to large differences in precipitation from December through June of these years.

Factors affecting twig growth. Precipitation influenced the amount of CSG produced. A linear relationship was found between current season's twig production by unbrowsed plants and the amount of precipitation received between December and June (Figure 6). Moisture received from December to mid-March recharged the soil profile prior to the initiation of plant growth, while precipitation received from mid-March to mid-June was used during the period of active plant growth. When precipitation was sufficient to wet the soil profile to the 20 cm depth, the zone of most abundant root biomass (Bowns 1973), increased production resulted.

Data obtained from heavily browsed blackbrush plants selected for intensive studies indicated that production of CSG was affected by soil depth and stoniness, utilization followed by rest, and branch location on the plant (Appendix Tables 20-23). Blackbrush plants growing on deep soils with little surface stone produced more CSG than plants growing on shallow soils with much surface stone

Table 9. Current season's twig production by blackbrush plants browsed at four stocking intensities.

	Current Season's Twig Production (mm · branch^{-1})		
	Year		
Pasture	1977[1/]	1978	1979
Control	85[a]	253[a]	230[a]
Light	81[a]	362[a]	314[a]
Moderate	84[a]	473[a]	426[a]
Heavy	195[b]	1005[b]	766[b]
Branch Location			
Terminal	118[c]	648[c]	610[c]
Basal	76[d]	264[d]	166[d]

[1/] Data from Provenza (1977).

[ab] Means in the same column followed by a different letter are significantly different (P=0.11, 0.07, and 0.10, for 1977, 1978, and 1979, respectively).

[cd] Means in the same column followed by a different letter are significantly different (P=0.13, 0.03, and 0.01 for 1977, 1978, and 1979, respectively).

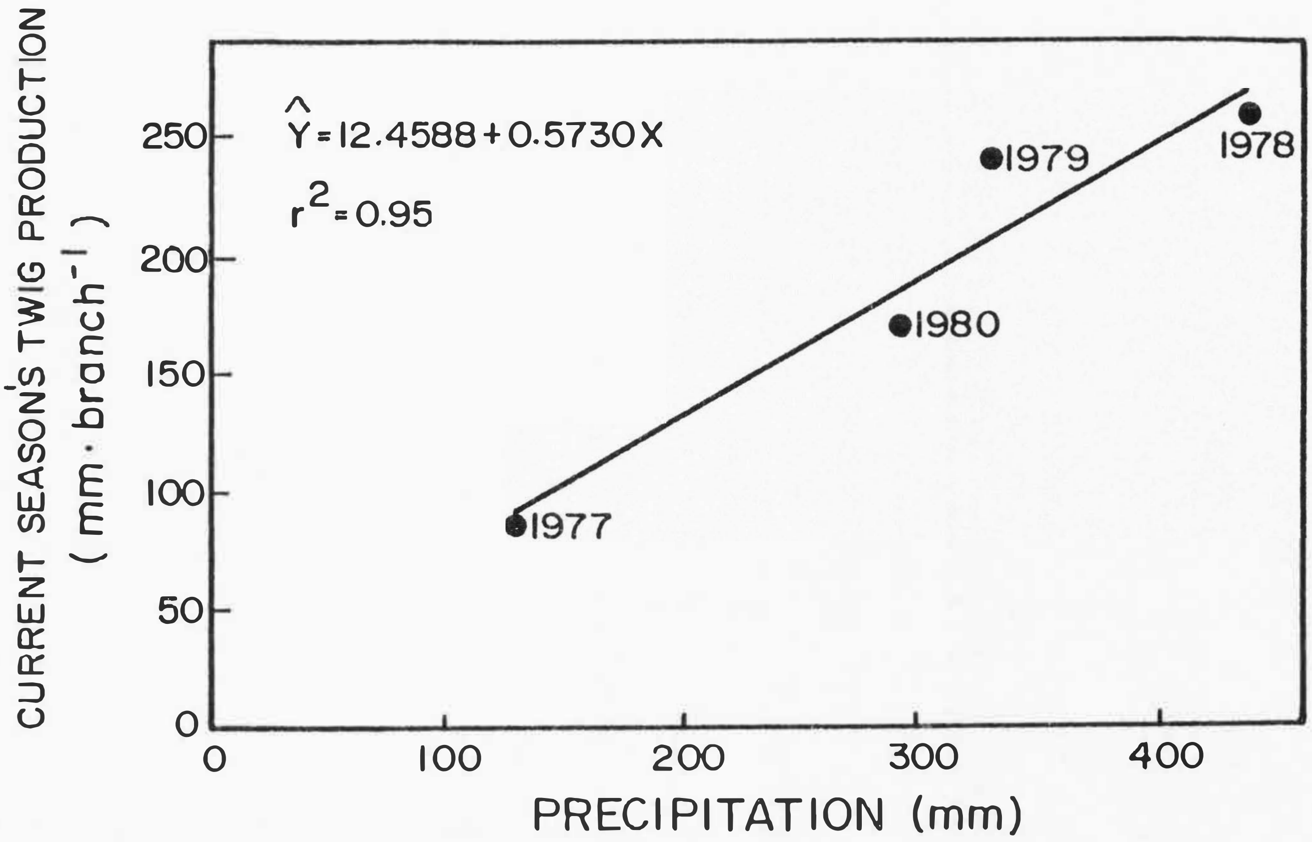


Figure 6. Relationship between the amount of precipitation received from December through June and current season's twig production by unbrowsed blackbrush plants.

(Table 10). The interaction between branch location and soil depth resulted from basal branches producing similar quantities of current season's twigs on deep and shallow soils, while the terminal branches of plants growing on deep soils outproduced those of plants growing on shallow soils.

Enhanced soil moisture relations were probably responsible for the increased twig production by plants growing on deep soils. Medin (1960) concluded that factors influencing soil moisture relations were key influences upon twig production in the shrub *Cercocarpus montanus*, and that as soil depth increased, more water was stored for use by plants.

The number of years of browsing and rest from browsing that blackbrush plants received also affected production of CSG (Figure 7). Browsing stimulated production of CSG by blackbrush, and even after four years, heavily browsed plants (greater than 95 percent of the CSG removed) still outproduced unbrowsed plants. A comparison of plants which were heavily browsed for four years with plants which were heavily browsed for one year (Figure 7, last two bars in 1980), indicated that current season's twig production did not decline as a result of heavy browsing. Abundant soil moisture during 1978 and 1979 likely increased the resistance of blackbrush to browsing. Nevertheless, the shrub appeared to be capable of survival with sustained twig removal. When browsing was terminated, however, production of CSG declined.

The data in Figure 7, when combined with a knowledge of how goats and cattle browsed blackbrush plants, provides implications for

Table 10. Current season's twig production by the terminal and basal branches of blackbrush plants growing on deep and shallow soils.

	Current Season's Twig Production ($mm \cdot branch^{-1}$)			
	Terminal Branches		Basal Branches	
Year	Deep Soils[1/]	Shallow Soils[1/]	Deep Soils[1/]	Shallow Soils[1/]
1977	528[a]	322[b]	152[a]	173[a]
1978	1616[a]	858[b]	377[a]	234[a]
1979	1396[a]	683[b]	158[a]	152[a]
1980	925[a]	444[b]	159[a]	106[a]

[1/] Average depth to the impervious caliche layer for deep and shallow soils was 71 cm and 39 cm, respectively.

[ab] Means in the same row, for a given branch location, are significantly different (LSD, $P<0.05$).

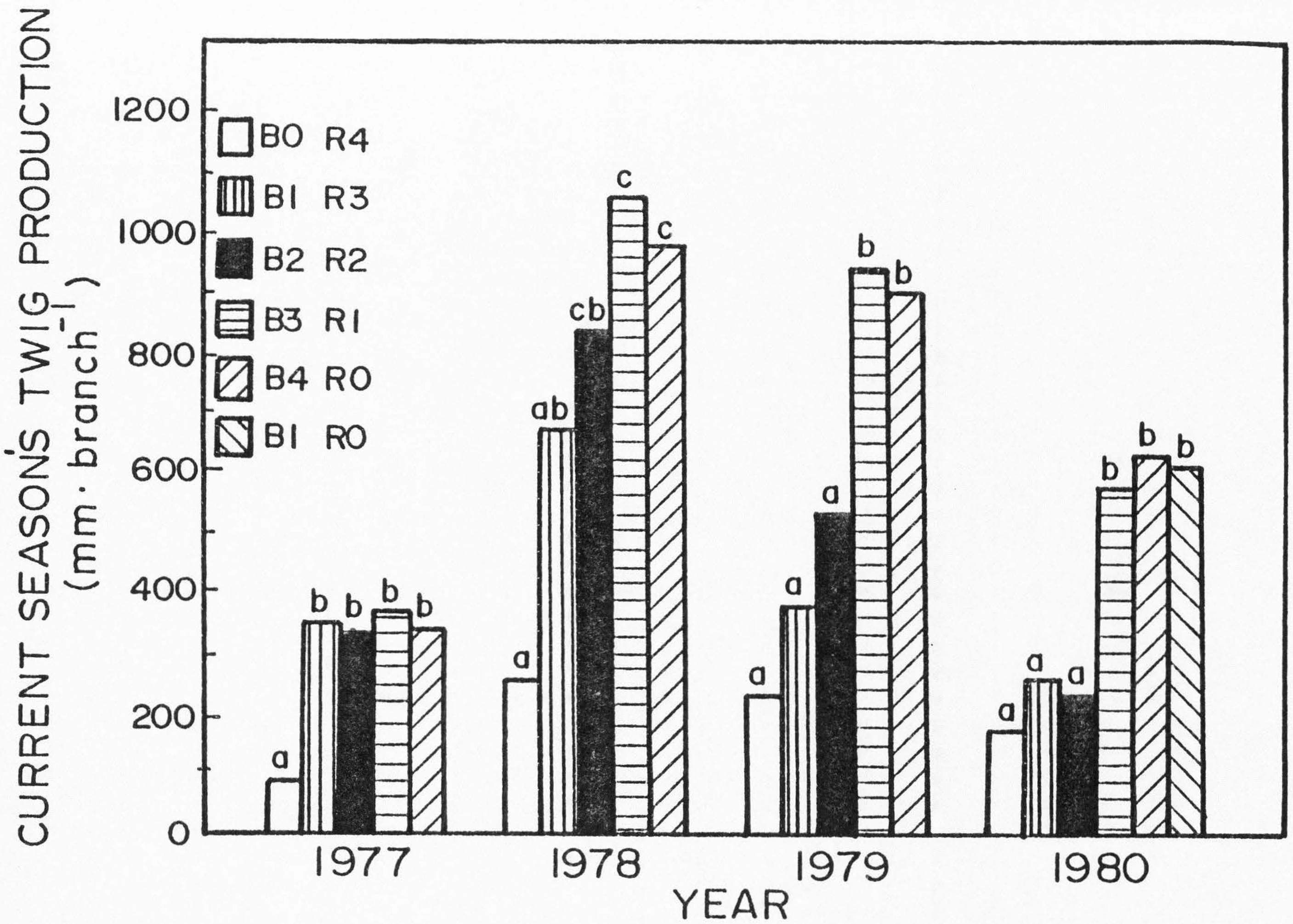


Figure 7. Current season's twig production by blackbrush plants. B and R represent browsed and rested from browsing and the numbers represent years. Letters above the bars represent statistically significant differences within years (LSD, P<0.05).

management. Blackbrush plants which were browsed and subsequently rested accumulated significant quantities of relatively new twig growth, while plants which were browsed without rest produced only current season's twigs (Table 11). When plants were browsed one year and rested for the next year or two, a larger quantity of more palatable twig material was available for consumption than when plants were browsed year after year. Factors relating to the palatability of blackbrush are discussed in a later section entitled "Anti-nutritional properties of twigs".

Older branches growing on the outer edges of blackbrush plants (terminal) were compared with sprouts and younger branches arising from within the plants canopy (basal) for production of CSG, and terminal branches outproduced basal branches (Table 10). Also, production of CSG by basal branches was not significantly different among the treatments, and terminal branches did not outproduce basal branches on control plants (Figure 8). The average leader length was longer for basal than terminal branches, which concurred with the finding of Bowns (1973) that the average leader length for basal twigs was twice that of terminal twigs. Twig production on heavily browsed plants, however, was primarily from terminal branches due to the large number of twigs produced.

Chemical

Nutritional properties of twigs. Analyses of hand-plucked blackbrush twigs representing material consumed by goats indicated that the nutrient content and digestibility of CSG on browsed plants

Table 11. Cumulative production of current season's twigs by blackbrush plants during a three year period.

Treatment	Current Season's Twig Production ($mm \cdot branch^{-1}$) 1977	1978	1979	Available for Consumption ($mm \cdot branch^{-1}$) 1978	1979
Browsed 1977, Rested 1978, 1979	345	676	384	1021	1405
Browsed 1977, 1978, 1979	341	974	903	974	903
Unbrowsed 1977, 1978, 1979	93	326	218	419	637

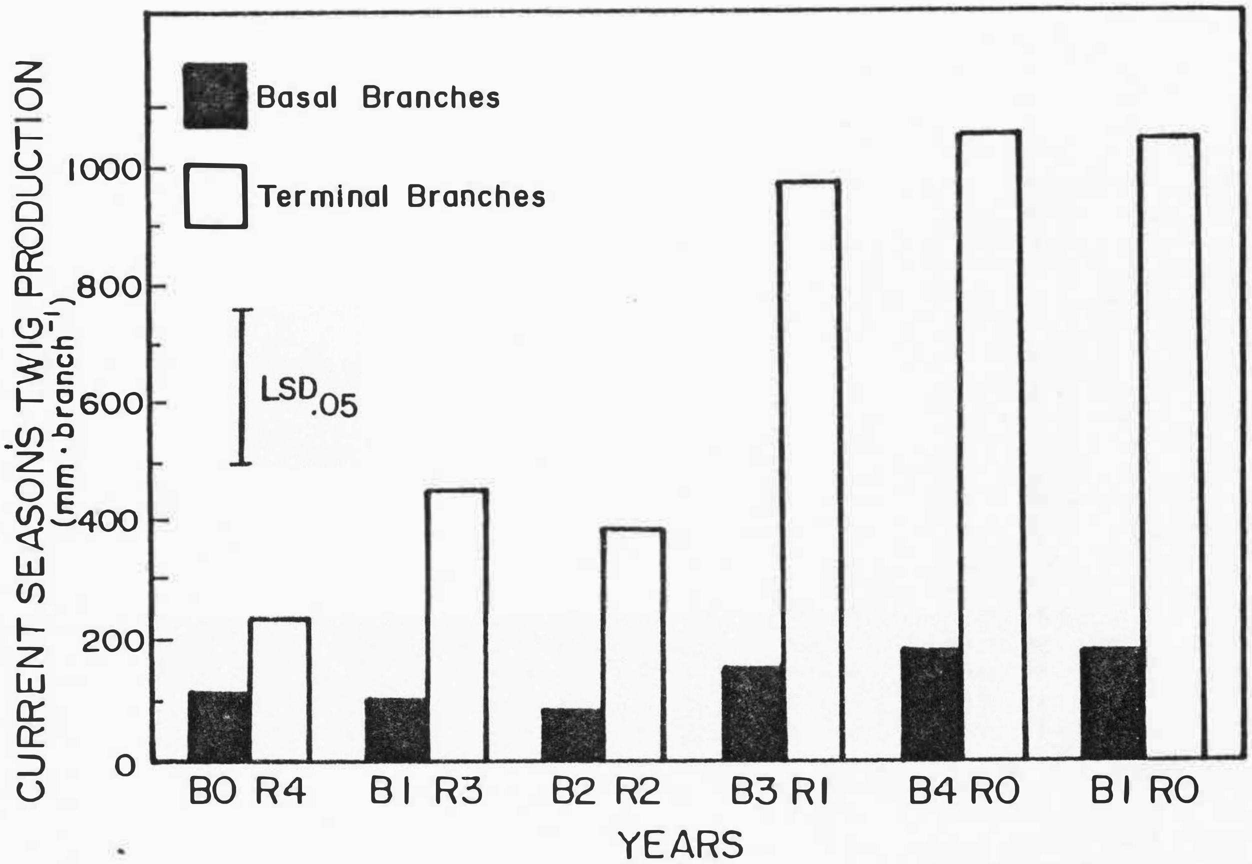


Figure 8. Current season's twig production by basal and terminal blackbrush branches in 1980. B and R represent browsed and rested from browsing and the numbers represent years.

was higher than that of older material on unbrowsed plants (Table 12, Appendix Tables 24-26). The crude protein and phosphorus contents of twigs collected in March of 1978 were higher than those of twigs collected in January of 1979. The fact that blackbrush generally begins growth in mid-March and was likely in a physiologically active state could account for this result, although blackbrush had not manifested signs of growth at the time these samples were collected.

Soil depth also affected the nutrient content of blackbrush, but differences were not highly significant (crude protein P=0.12, phosphorus P=0.11) due to the low number of error degrees of freedom. Plants growing on deep soils tended to contain more nutrients than those growing on shallow soils. Perhaps greater soil depth permitted better soil moisture relations, improving nutrient uptake by the plants. Harner and Harper (1973) stated that improved soil moisture relations enhance the mineral status of soils by accelerating microbial action which causes the release of essential elements. Their data showed that soil moisture and the nutrient content of vegetation were closely related. In this connection, Bhaumik and Clark (1947) indicated that decomposer organisms of the soil performed optimally at moisture levels near field capacity if aeration and temperature were favorable, and Moser and Olson (1953) indicated that as soil dries, the activity of soil organisms declines rapidly.

Basal branches were higher in crude protein and more digestible than terminal branches (Table 13, Appendix Tables 27-28). Basal branches had a higher leaf:stem ratio and appeared to be less fibrous than terminal branches, which may account for their higher

Table 12. Percent crude protein, phosphorus, and in vitro dry-matter digestibility (IVDMD) for current season's and older twigs from the terminal branches of blackbrush plants growing on deep and shallow soils.

Assay	Twig Age		Plant Location		Year	
	Current Growth	Older Growth	Deep Soils	Shallow Soils	March 1978	January 1979
Crude Protein	6.5[a]	4.6[b]	5.9[a]	5.2[b]	6.2[a]	4.9[b]
Phosphorus	0.10[a]	0.08[b]	0.10[a]	0.08[b]	0.11[a]	0.08[b]
IVDMD	47.7[a]	38.2[b]	42.7[a]	43.1[a]	44.3[a]	41.6[a]

[ab] Means in the same row, for a given twig age, plant location, or year, followed by a different letter are significantly different (for twig age, crude protein, and IVDMD $P<0.05$, phosphorus $P<0.10$; for plant location, crude protein $P=0.12$, phosphorus $P=0.11$; for year, crude protein and phosphorus $P<0.05$).

Table 13. Percent crude protein and in vitro dry-matter digestibility (IVDMD) for current season's twigs from terminal and basal blackbrush branches.

Assay	Twig Location	
	Terminal Branch	Basal Branch
Crude Protein	5.7[a]	6.1[b]
IVDMD	41.1[a]	44.2[b]

[ab]Means in the same row followed by a different letter are significantly different (P=0.10 and 0.05 for crude protein and IVDMD, respectively).

nutrient content and digestibility. Bowns (1973) indicated that blackbrush leaves were higher in crude protein and lower in acid detergent fiber than stems.

Anti-nutritional properties of twigs. Although CSG was higher in nutrients and more digestible than older twigs, this material contained high tannin levels (Figure 9, Appendix Table 29). Absorbance values of 0.9 were considered high by Hagerman and Butler (1978). Twigs collected for tannin analysis simulated material available to goats and cattle browsing in different blackbrush pastures. As such, the terminal branches of control plants (B0R4) were primarily old growth while basal branches were composed of current season's and older growth (control pastures). The terminal and basal branches of plants which were browsed without rest (B1R0, B4R0) were composed entirely of CSG (heavily stocked pastures), and the terminal and basal branches of plants which were browsed and subsequently rested (B3R1, B2R2, B1R3) were composed of a mixture of current season's and older growth (moderate and lightly stocked pastures).

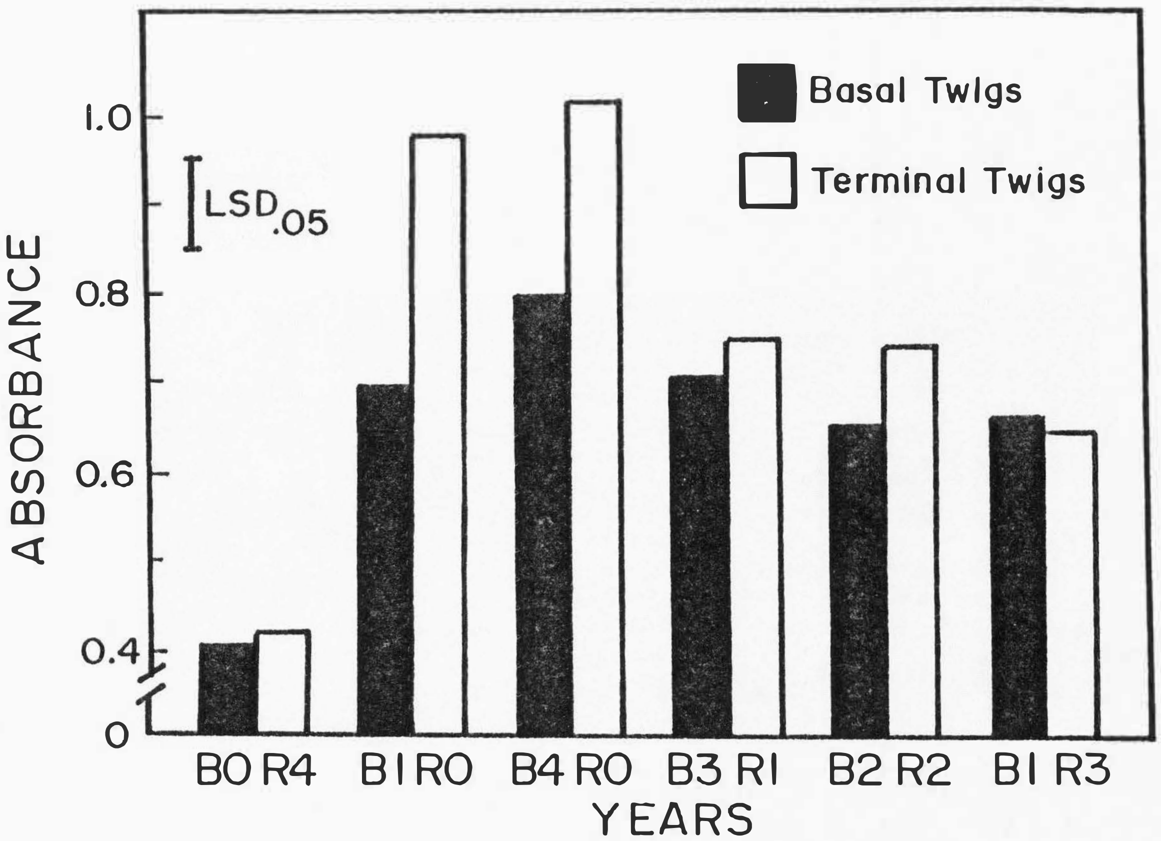


Figure 9. Tannin levels in twigs growing on the terminal and basal branches of blackbrush plants. B and R represent browsed and rested from browsing and the numbers represent years.

Control plants contained relatively low tannin levels, while plants which were browsed without rest contained high tannin levels. Also, the terminal branches of plants browsed without rest contained considerably higher tannin levels than basal branches. With rest from browsing, tannin levels decreased due to the decreased proportion of current season's to older growth. The "disappearance" of tannins from older twigs probably resulted from their increased polymerization to compounds of high molecular weight (Goldstein and Swain 1963, Joslyn and Goldstein 1964) which were no longer active as protein complexers.

The relative proportion of current season's to older growth varied on blackbrush plants during this study. This affected tannin levels and probably affected goat and cattle diet selection. Study pastures were browsed initially by Angora goats in 1977; however, low utilization (Table 7), coupled with a paucity of moisture (Figure 6), resulted in scant production of CSG (Figure 7). Heavy utilization levels in 1978 by supplemented Spanish goats, coupled with abundant moisture, resulted in large productions of CSG by terminal and basal branches in the heavily stocked pastures (Table 9). Therefore, goats browsing in the heavily stocked pastures in 1979 were forced to select CSG on either terminal or basal branches, and goats preferred basal branches (Table 7). Heavy stocking intensities during the cattle study resulted in high levels of utilization on terminal and basal branches in the control and heavily stocked pastures, however, cattle browsing in the lightly and moderately stocked pastures tended to prefer basal branches.

The selective response of goats and cattle browsing blackbrush plants was likely affected by varying tannin levels, the coarseness of the twigs, and the spinescent growth form. For plants browsed without rest, high tannin levels in the CSG produced by terminal branches probably reduced their palatability relative to basal branches (Figure 9). Although the CSG produced by terminal branches was unpalatable to goats and cattle, when these twigs were rested from browsing their palatability increased, presumably due to decreased tannin levels (Figure 9). Hand-plucked samples were also more difficult to harvest from terminal than basal branches. Terminal branches were coarser and required greater effort to remove than the lax basal branches which broke with little effort. Goats and cattle browsing moderately and lightly stocked pastures tended to prefer basal branches to spinescent terminal branches (Table 7, 1978 goat utilization for all pastures and 1979 cattle utilization data for lightly and moderately stocked pastures).

Terminal branches posed a physical barrier to animals browsing basal branches (Figure 5). However, goats and cattle selected basal branches, in spite of their location within the terminal branch canopy, and much lower biomass relative to the terminal branches. This was viewed as an indication of the strength of their selective response. The hair abra-ded from the nose of the Angora goat in Figure 10 was typical of goats' and cattles' appearance as a result of browsing basal branches.

High plant-to-plant variability in utilization levels, which subsequently affected twig production, was probably related to

Figure 10. Angora goat with the hair abra-ded from it's nose as a result of browsing basal branches on blackbrush plants.

variability in spinescence (Figure 5) and tannin levels. Extremely spinescent plants, and presumably plants with high tannin levels, were avoided by goats and cattle, and the relationship between spinescence and tannin levels merits further investigation (i.e., if spinesence and tannins are defenses, spinescent plants may contain lower levels of tannins). Among heavily browsed blackbrush plants, tannin levels in CSG varied greatly, but terminal branches always contained higher tannin levels than basal branches. For example, one blackbrush plant contained tannin levels (absorbance values) of 1.3 and 1.0 in terminal and basal twigs, respectively, while another plant contained levels of 0.8 and 0.2.

Soil depth also affected tannin levels in blackbrush twigs, but terminal twigs responded differently than basal twigs (Figure 11). Terminal twigs contained higher tannin levels on deep soils, while basal twigs contained similar tannin levels on deep and shallow soils.

Further examination revealed that tannin levels in the leaves of terminal and basal twigs were similar, while terminal twigs were much higher in tannins than basal twigs (Figure 12, Appendix Table 30). This, coupled with the fact that the weight ratio of leaf:stem for basal twigs (0.59) was higher than that for terminal twigs (0.36), resulted in higher tannin levels in terminal than basal twigs.

The occurrence of tannins in blackbrush is interesting from a theoretical, as well as practical, point of view. Blackbrush data tend to support Rhoades (1979) hypotheses dealing with

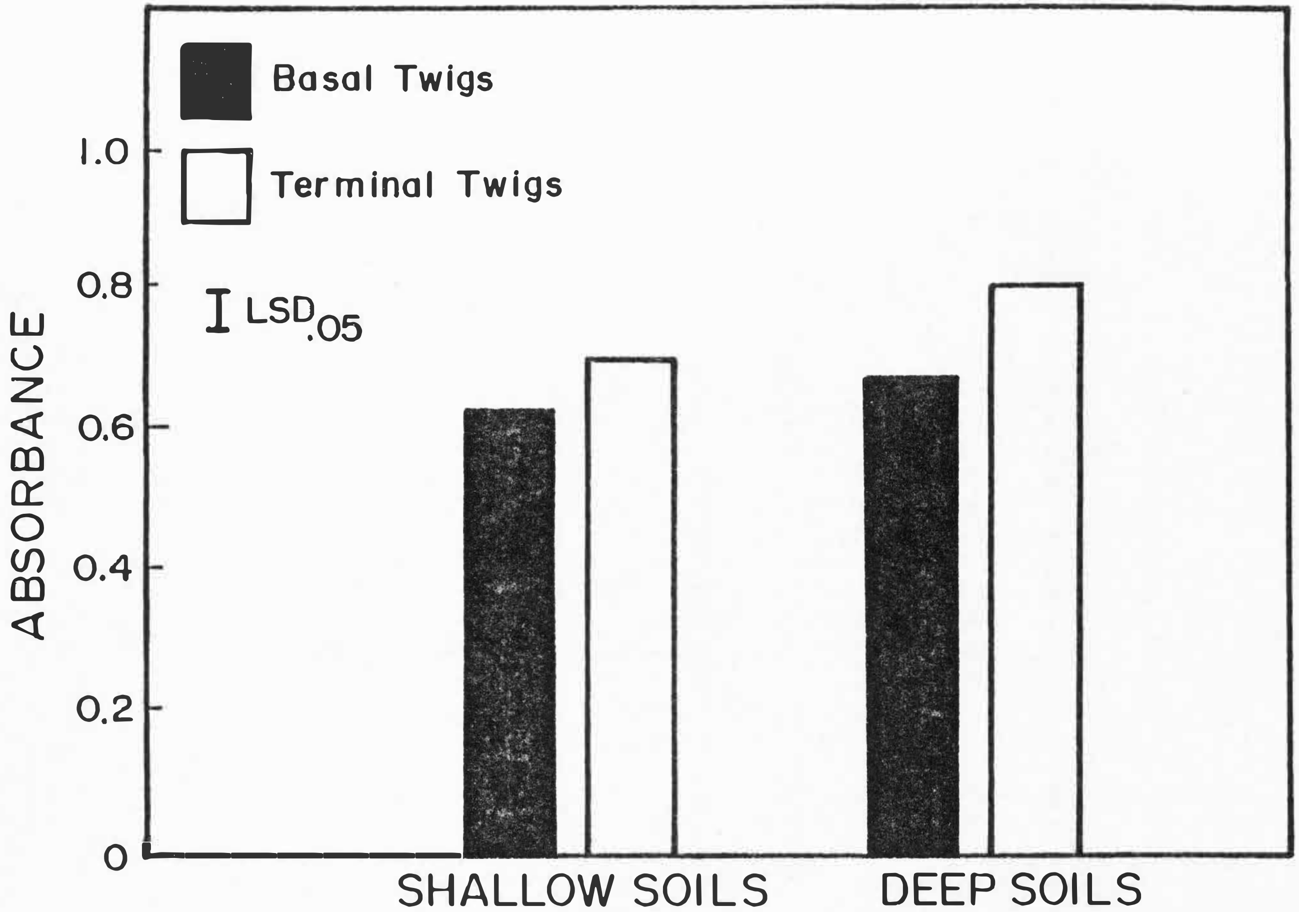


Figure 11. Tannin levels in the basal and terminal twigs of blackbrush plants growing on shallow and deep soils.

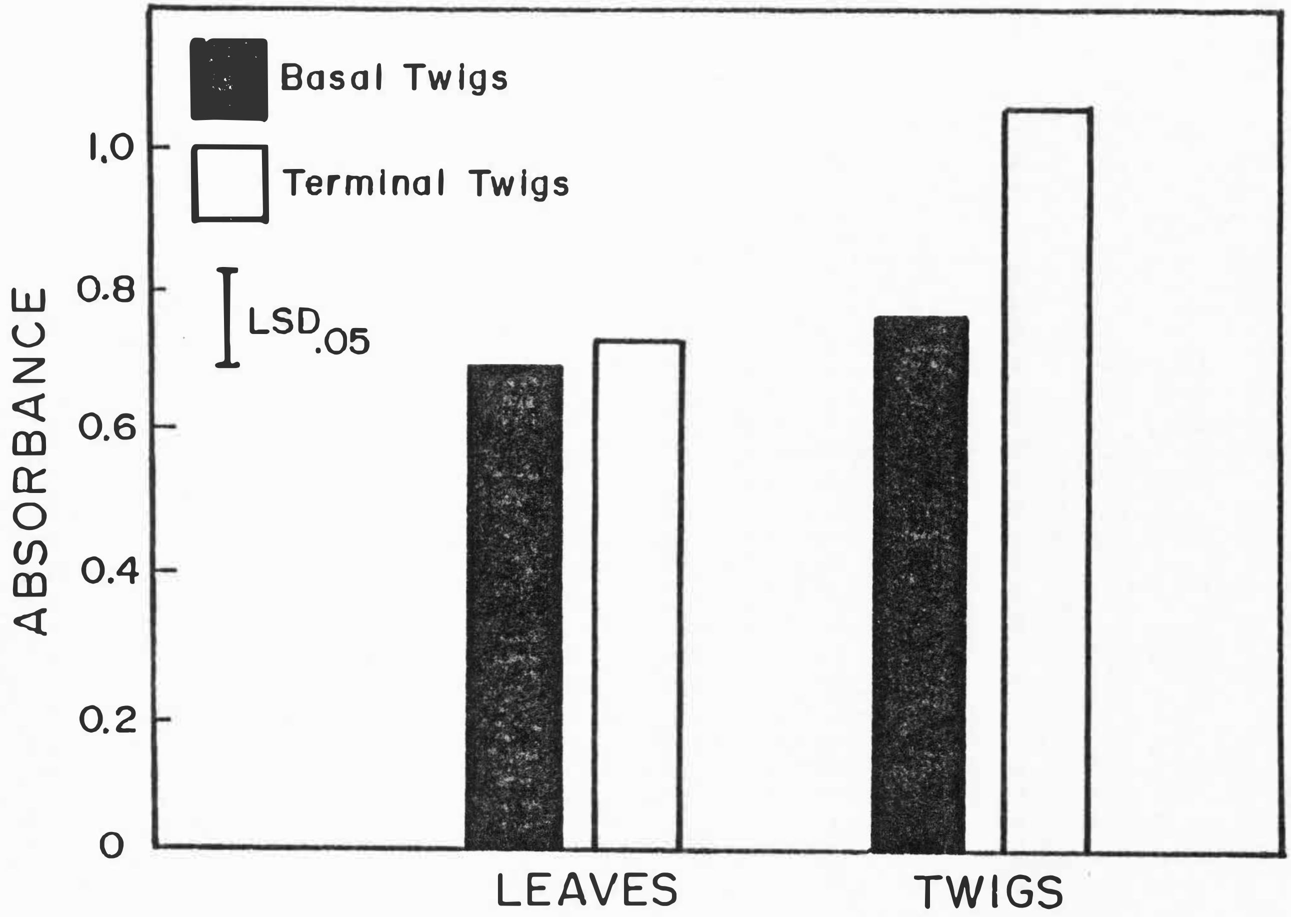


Figure 12. Tannin levels in the leaves and twigs of basal and terminal blackbrush branches.

elaboration and allocation of phyto-chemicals as defense mechanisms against herbivores. If tannins are costly to produce and play a role in plant defense, commitment to defense should decrease when herbivores are absent and increase when plants are subjected to herbivory (hypothesis 3). Unbrowsed blackbrush plants could conceivably accomplish this in two ways: (1) decrease the quantity of tannins in CSG, and/or (2) decrease the quantity of CSG. As previously illustrated (Figure 7), unbrowsed blackbrush plants produced little CSG, even in years of abundant moisture, and as a result their twigs were low in tannin levels (Figure 9). Once browsed, branches responded by producing new twigs which were high in tannins; however, only browsed branches increased twig production.

Blackbrush data did not tend to support Rhoades (1979) hypothesis that physical plant stress results in an increase in proximate nutritional quality and a decrease in the quantity of defense (hypothesis 4). Rather, blackbrush plants growing on shallow soils, presumably under stressful conditions, contained lower nutrient (Table 12) and tannin (Figure 11) levels than twigs produced by plants growing on deep soils.

Within heavily browsed blackbrush plants, less tannins were allocated to basal than terminal twigs. In referring to Rhoades (1979) second hypothesis, which relates to the susceptibility of different plant parts to herbivory, one must realize that the herbivore(s) which influenced blackbrush evolution possibly had different browsing habits from goats and cattle, and were not confined to small pastures. Terminal and basal branches have discovery rates dependent on the herbivore, as well as twig density and location. If a plant part is discovered, mechanical defenses such as silica, calcium carbonate, and spinescence, as well as one or more types of chemical defense, influence herbivory.

During evolutionary time, basal branches may have been less prone to herbivory than terminal branches due to their lower biomass and seemingly protected location within the plant (Figure 5). Also, due to their lower biomass and shaded location within the plant, basal branches may produce less photosynthate than terminal branches and thus represent a smaller loss to the plant if removed occasionally. However, basal branches eventually replace senescent terminal branches and repeated removal of basal branches would eventually result in death of the plant.

From this standpoint, the effect of basal branch removal on subsequent tannin levels is interesting. If blackbrush plants are capable of responding to herbivory, one would hypothesize that tannin levels in basal branches would increase as the number of living terminal branches decreased due to senescence. In this light, the trend toward increased tannin levels in the basal branches of plants browsed heavily for four years (B4RO) versus plants browsed for one year (B1RO) is curious (Figure 9), and lends support to the hypothesis posed above.

Within blackbrush branches, fewer tannins were allocated to leaves than twigs (Figure 12). Three possible explanations for this finding are:

1. Tannins, as well as lignin, play a role in preventing fungal and microbial decomposition of supporting structures in woody plants (Swain 1979), and would be expected in higher concentrations in stems.

2. Blackbrush leaves may possess fewer storage locations for tannins due to their small size and physiological function in photosynthesis. Due to this function leaves are high in enzymes which could complex with tannins unless stored separately (McKey 1979).

3. Although blackbrush is an evergreen, some leaves are shed on an annual basis (Bowns 1973), while stems are persistent. As a result, tannin allocation to leaves is more expensive (Rhoades 1979).

Response of Goats to Blackbrush Manipulation

Comparison of does and kids

Diets. The diet sample results are presented graphically by pasture (heavy versus light) and age class (does versus kids) to illustrate trends common to the botanical, chemical, and activity budget data collected in 1979. However, statistically significant pasture X date or age class X date interactions are not implied. When these interactions are significant, the least significant difference (LSD) is indicated on the graph. Statistically significant differences in main effects and interactions are indicated in the Appendix and are discussed in the text.

Due to the paucity of other plant species in the community, blackbrush was the primary dietary item (Figures 13 and 14). Goats

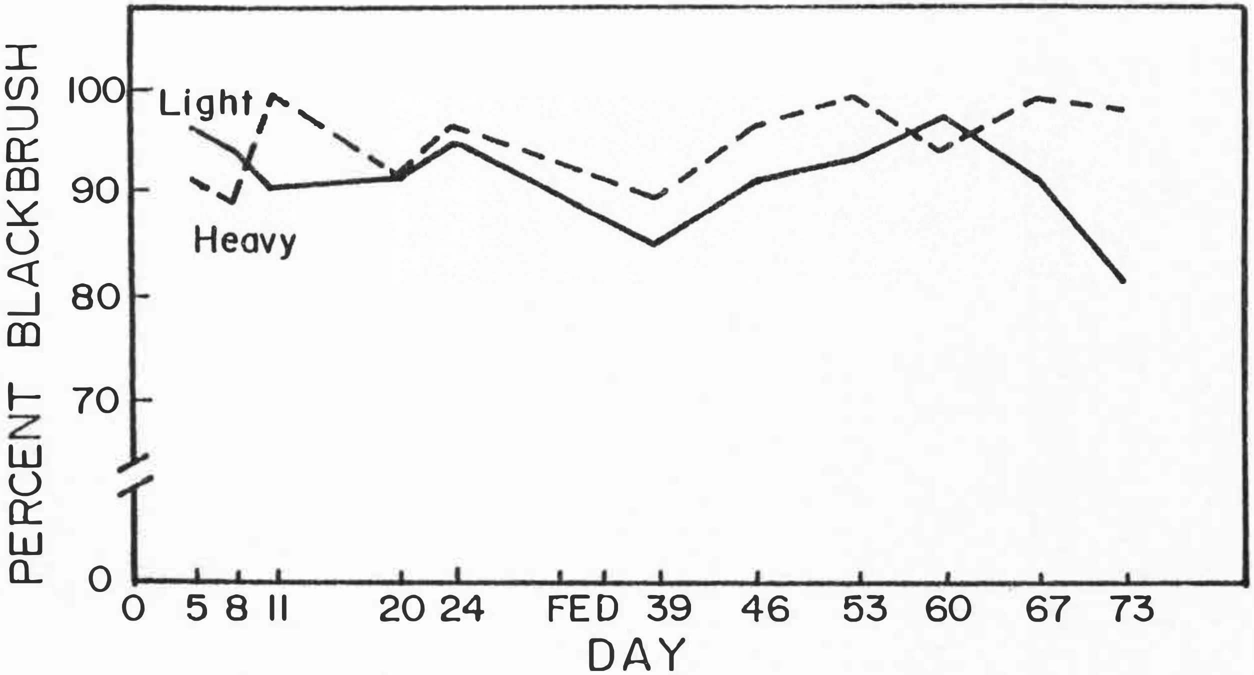


Figure 13. Percent blackbrush in the diets of esophageally fistulated goats browsing in lightly and heavily stocked pastures from January 2 until March 17 of 1979.

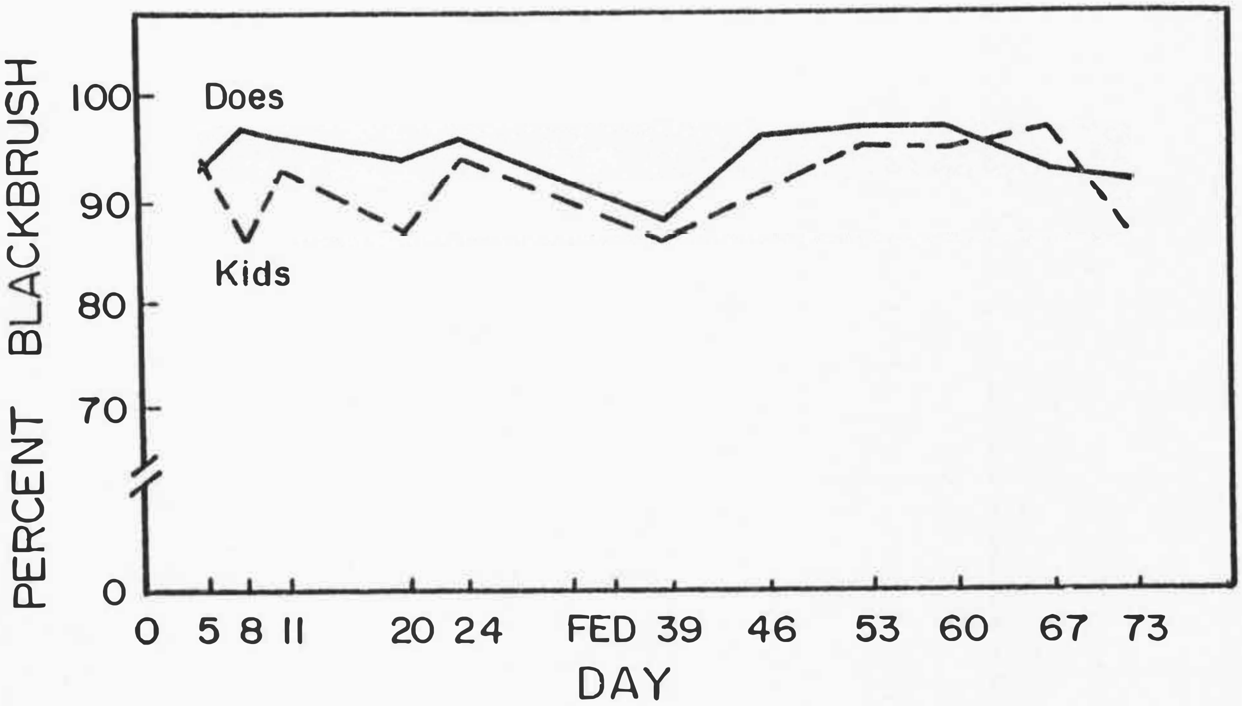


Figure 14. Percent blackbrush in the diets of esophageally fistulated does and kids browsing in pastures from January 2 until March 17 of 1979.

consumed somewhat more blackbrush in the heavily than in the lightly stocked pasture and does consumed more blackbrush than kids (Appendix Table 31). During the first part of the browsing period, dried grasses and forbs, juniper, pinyon, and desert peachbrush were consumed with blackbrush. On days 29 and 30 of the study, a snowstorm covered the blackbrush plants, so the animals were supplemented with alfalfa hay. As a result, small quantities of hay appeared in the diet samples for days 39 and 46.

Twigs from terminal and basal branches could not be ascertained separately from direct analysis of fistula extrusa. However, this was estimated indirectly, based on the difference in leaf:stem ratios of terminal and basal twigs. A small sample (n = 6) of current season's twigs collected from terminal and basal branches had leaf: stem ratios of 0.36 gm ± 0.07 gm and 0.59 gm ± 0.12 gm (means ± 95 percent confidence limits), respectively. These data provided a reference for the botanical anlaysis, since higher leaf:stem ratios indicated a greater proportion of basal branches in the sample. The regression equation in Figure 15 was used to convert leaf:stem ratios based on hits to weight ratios. Subsamples within each standard varied, lowering the coefficient of determination (r^2).

The leaf:stem ratios for goats browsing in the heavily and lightly stocked pastures are presented in Figure 16 (Appendix Table 32). For goats that browsed in the heavily stocked pasture, leaf: stem ratios generally declined during the browsing period, presumably due to the decreasing quantity of basal branches. For goats that browsed in the lightly stocked pastures, leaf:stem ratios were low

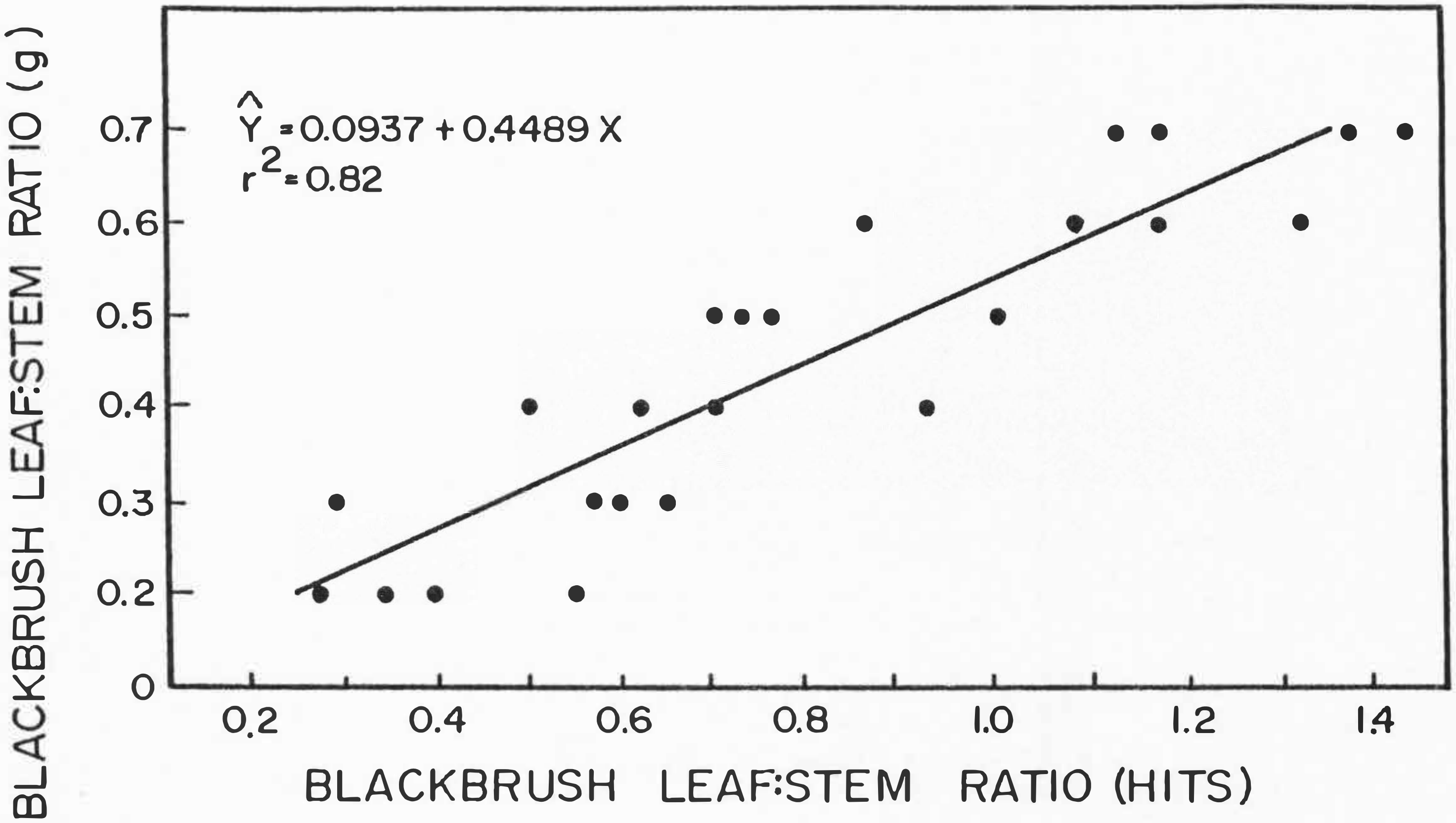


Figure 15. Regression relationship used to convert blackbrush leaf:stem ratios based on hits to weight ratios.

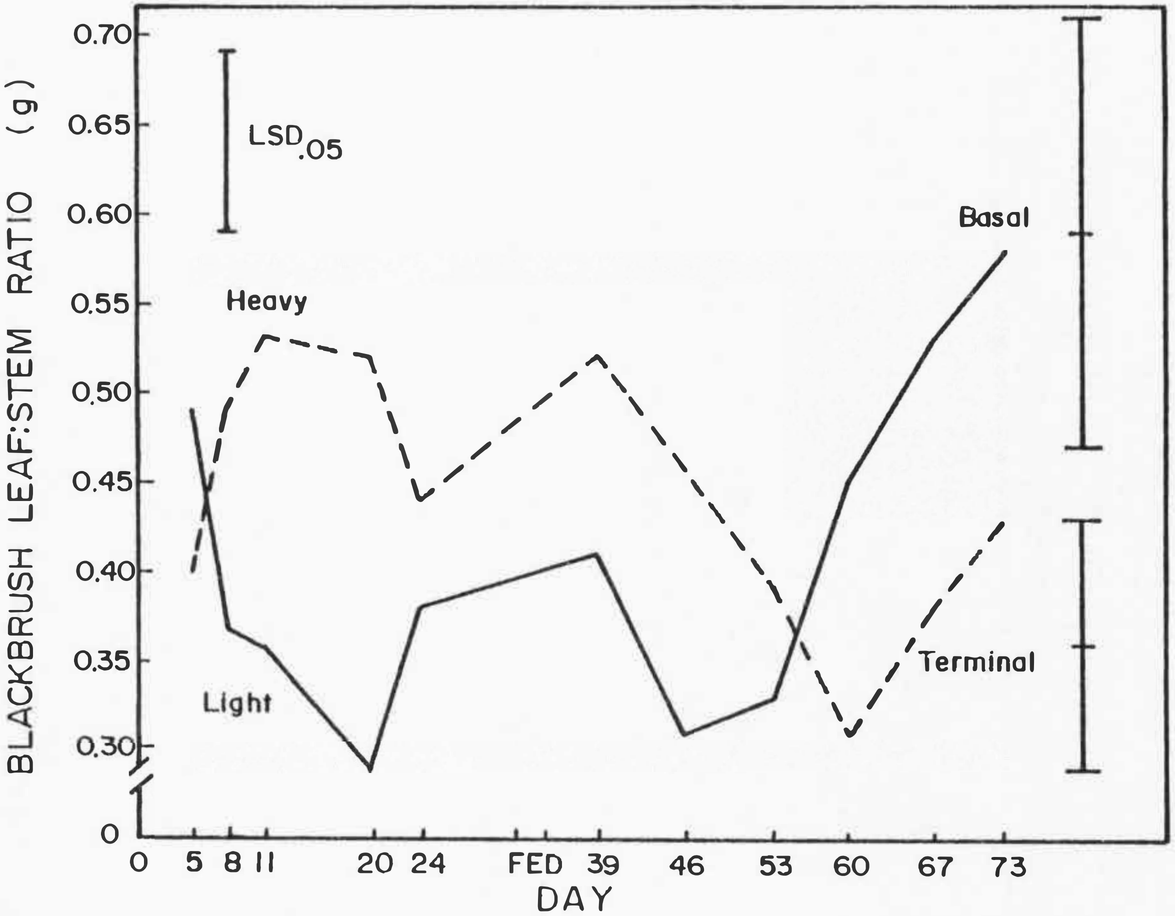


Figure 16. Leaf:stem ratios for blackbrush in the diets of esophageally fistulated goats browsing in heavily and lightly stocked pastures from January 2 until March 17 of 1979. The ratio of leaf:stem (mean ± 95% confidence limits) for basal and terminal twigs is illustrated on the right side of the graph.

during most of the study, but increased during the last three weeks. Assuming older twigs growing on the terminal branches of blackbrush plants had leaf:stem ratios similar to, or lower than, those of current season's twigs, the goats that browsed in the lightly stocked pasture selected for older twigs growing on terminal branches early in the browsing period, and for basal branches later in the browsing period.

Mastication decreased the tannin levels in samples collected from esophageally fistulated goats (Table 14, Appendix Table 33), presumably as a result of tannins complexing with proteins in the goat saliva and plant tissues. In vitro organic-matter digestibility was also decreased as a result of mastication (Table 14, Appendix Table 34). The ability of rumen microorganisms to degrade proteins and carbohydrates may have been reduced as a result of tannins complexing the proteins and carbohydrates in the plant tissues (McLeod 1974, Basaraba and Starkey 1966).

The statistically significant interaction between branch location and mastication is interesting. If tannins were involved in depressing digestiblity, terminal twigs should have inhibited digestion more than basal twigs, due to their higher tannin content. With dealing with tannins, a 1:1 relationship between digestibility in vitro and in vivo may not exist unless samples are masticated prior to anlaysis, since this allows tannins to complex with proteins and carbohydrates. Nastis (1977) studied the relationship between in vitro and in vivo digestibility for oakbrush (Quercus gambelii), a species containing high tannin levels. He found a significant

Table 14. Tannin and in vitro organic-matter digestibility (IVOMD) values (mean ± 95% confidence interval) for terminal and basal twigs of masticated and unmasticated blackbrush samples.

Assay	Terminal Twigs[1]			Basal Twigs[1]		
	Unmasticated	Masticated	Ratio (masticated: unmasticated)	Unmasticated	Masticated	Ratio (masticated: unmasticated)
Tannins[2]	1.14±0.12	0.53±0.12	0.47	0.84±0.12	0.43±0.12	0.51
IVOMD[2]	36.1±1.4	28.0±1.4	0.78	41.2±1.4	35.8±1.4	0.87

1/ Samples consisted entirely of current season's growth.

2/ Due to slight soil contamination of some samples, results were expressed on an organic matter basis.

relationship (r^2 = 0.97) between in vitro and in vivo digestibilities, but in vitro digestibilities over-estimated in vivo digestibilities. Further research is necessary concerning the effects of tannins on in vitro and in vivo digestibilities.

Assuming 50 percent of the originally active tannins in the goat diet samples were detected (Table 14), tannin levels in Figure 17 are half of what they were when the goats consumed the twigs. Absorbance values of about 0.4 would be expected for older twigs, while values of about 0.7 and 1.0 would be expected for current season's twigs collected from basal and terminal branches, respectively. Goats, however, selected plants and plant parts that were considerably lower in tannins than those which were clipped.

Goats browsing in the heavily stocked pasture consumed twigs which contained higher tannin levels than goats browsing in the lightly stocked pasture (Appendix Table 35), because goats browsing in the heavily stocked pasture were forced to consume larger quantities of CSG. Tannin levels in the diets of goats browsing in the lightly stocked pasture declined later in the browsing season due to the increased leaf:stem ratios and increased quantity of green grasses and forbs. Due to the small pasture size, fewer green grasses and forbs were available to goats browsing in the heavily stocked pasture. Thus, the general decline in tannin levels probably resulted from increased selection for low-tannin plant parts.

Crude protein levels in the diets of goats browsing heavily and lightly stocked pastures followed a trend similar to the leaf:stem ratio data (Figure 18). Goats browsing in the heavily stocked

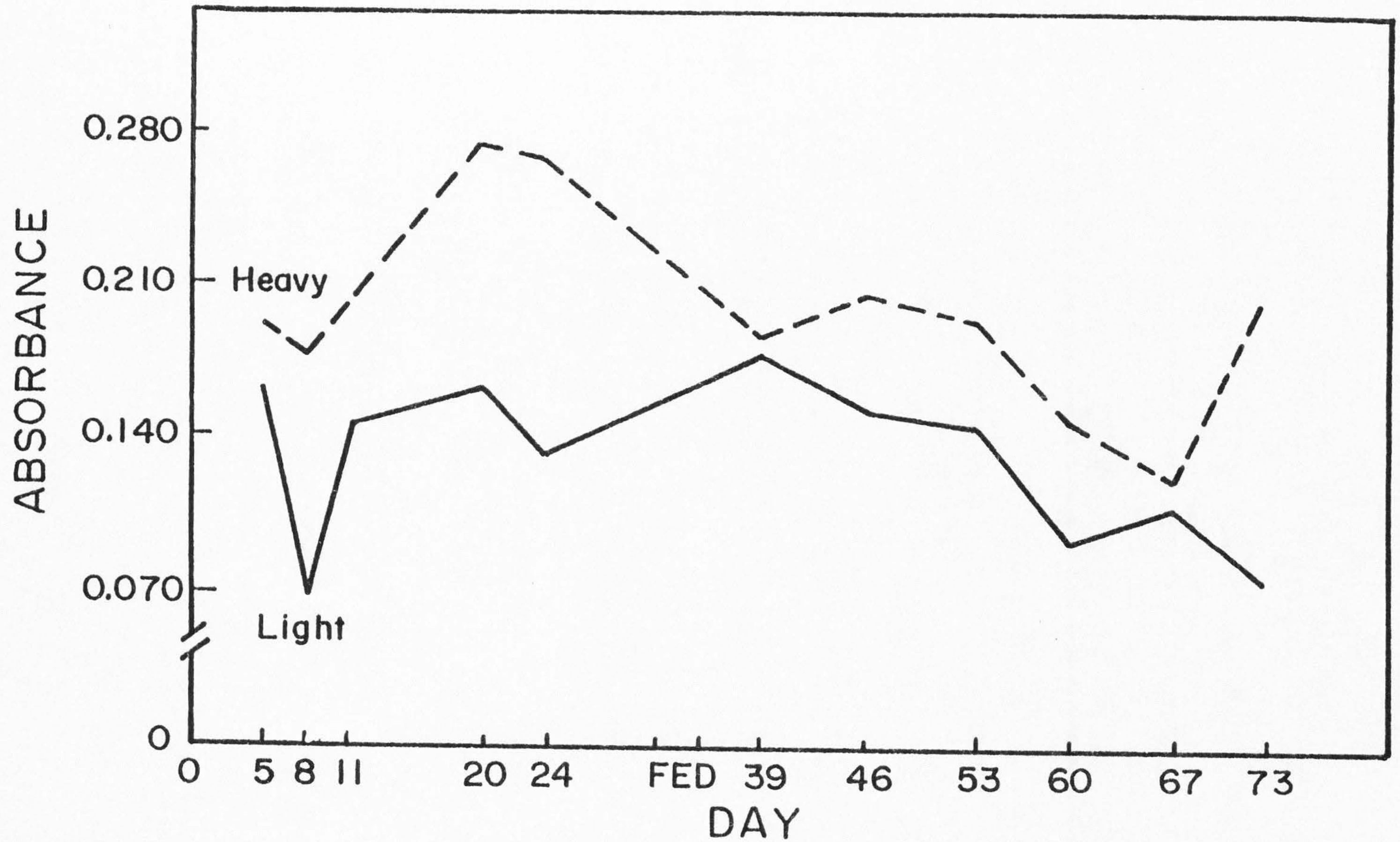


Figure 17. Tannin levels in the diets of esophageally fistulated goats browsing in heavily and lightly stocked blackbrush pastures from January 2 until March 17 of 1979.

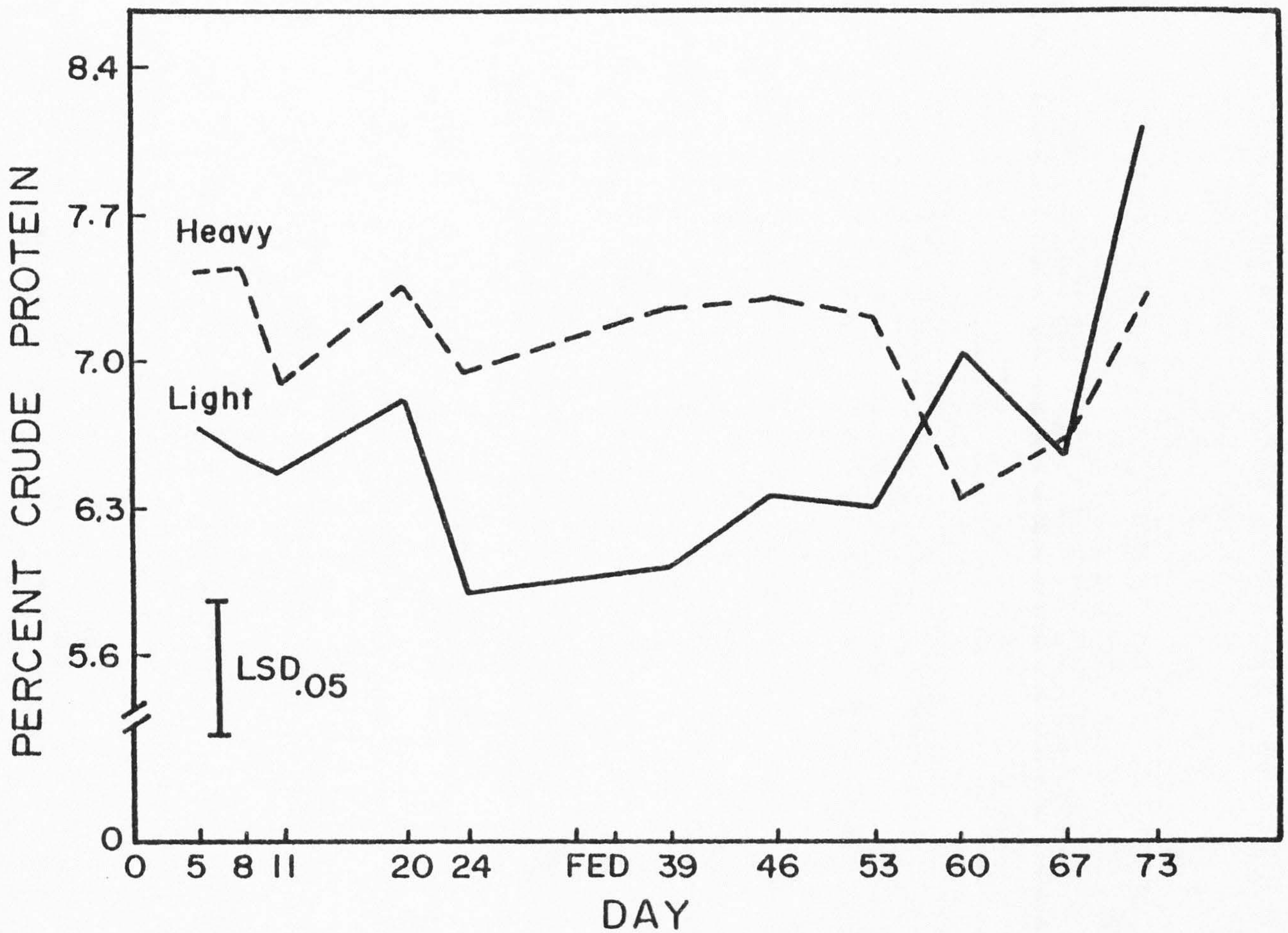


Figure 18. Percent crude protein in the diets of esophageally fistulated goats browsing in heavily and lightly stocked blackbrush pastures from January 2 until March 17 of 1979.

pasture consumed diets higher in crude protein (Appendix Table 36), due to higher leaf:stem ratios and more CSG. The increased crude protein levels near the end of the grazing period for goats foraging in the lightly stocked pasture resulted from increased leaf:stem ratios and increased consumption of green grasses and forbs.

In vitro dry-matter digestibility (IVDMD) values also followed a trend similar to the leaf:stem ratio data (Figure 19, Appendix Table 37). In general, IVDMD values were higher for animals browsing CSG in the heavily stocked pastures. On days 39 and 46, however, animals browsing in the lightly and heavily stocked pastures had high IVDMD values, presumably as a result of eating alfalfa. Toward the end of the study, IVDMD values increased due to increased leaf:stem ratios and increased levels of green forbs and grasses in the lightly stocked pasture, and increased leaf:stem ratios in the heavily stocked pasture.

Though not highly significant, does consumed diets with higher leaf:stem ratios during the first part of the study, while kids consumed diets with higher leaf:stem ratios during the latter part of the study (Figure 20, Appendix Table 32). This interaction may have resulted from greater selection by the kids as they gained experience browsing blackbrush.

Tannin levels in diets selected by does and kids were not different statistically (Figure 21, Appendix Table 35). If tannins were an overriding factor in determining diet selection by does and kids, however, differences should not be expected. The lower tannin

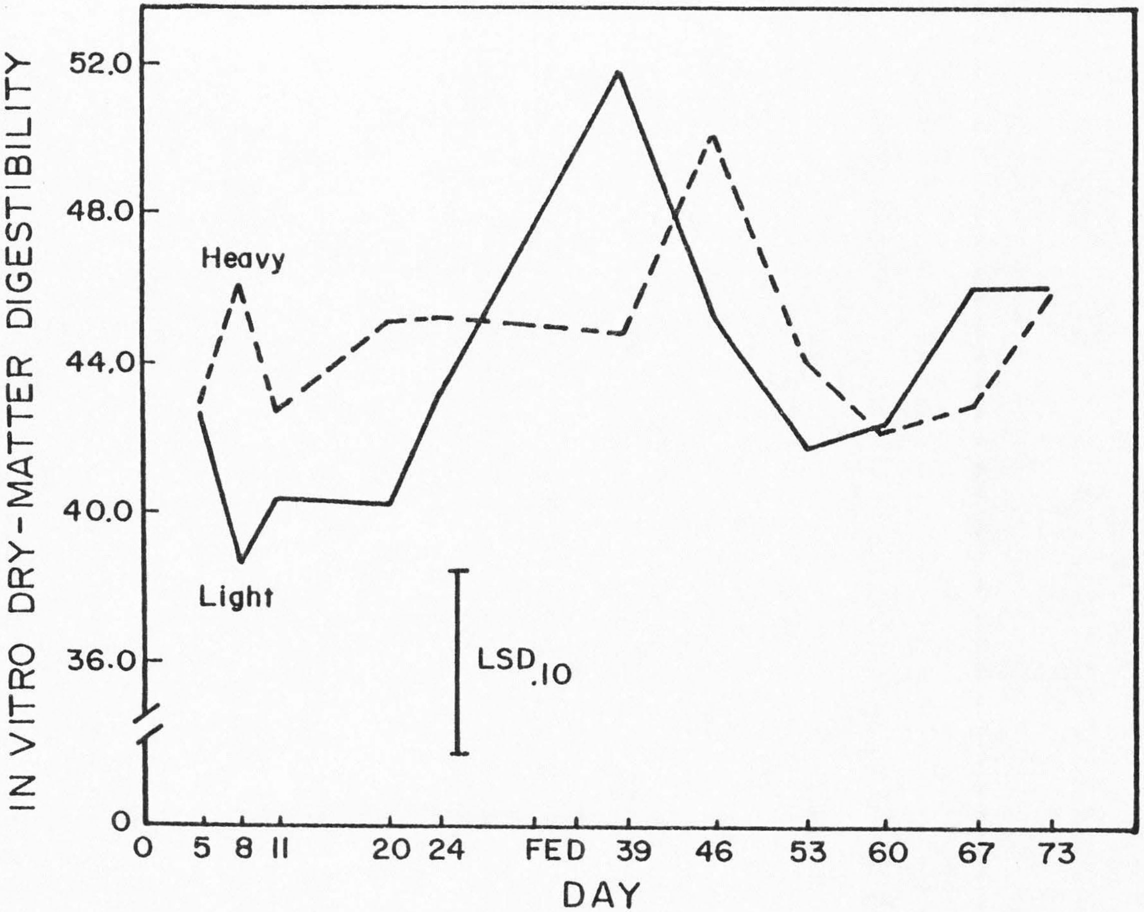


Figure 19. In vitro dry-matter digestibility of diets consumed by esophageally fistulated goats browsing in heavily and lightly stocked blackbrush pastures from January 2 until March 17 of 1979.

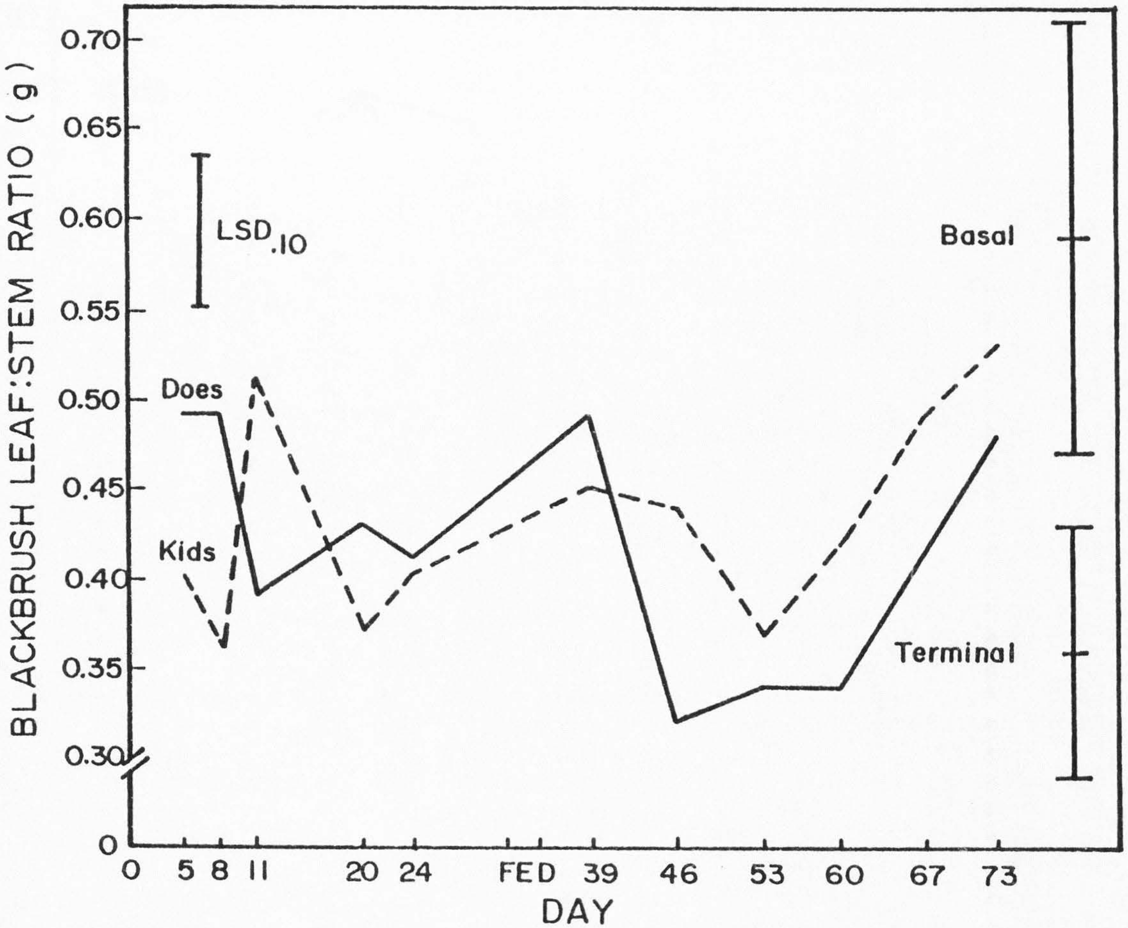


Figure 20. Leaf:stem ratios for blackbrush in the diets of esophageally fistulated does and kids browsing in pastures from January 2 until March 17 of 1979. The ratio of leaf:stem (mean ± 95% confidence limits) for basal and terminal twigs is illustrated on the right side of the graph.

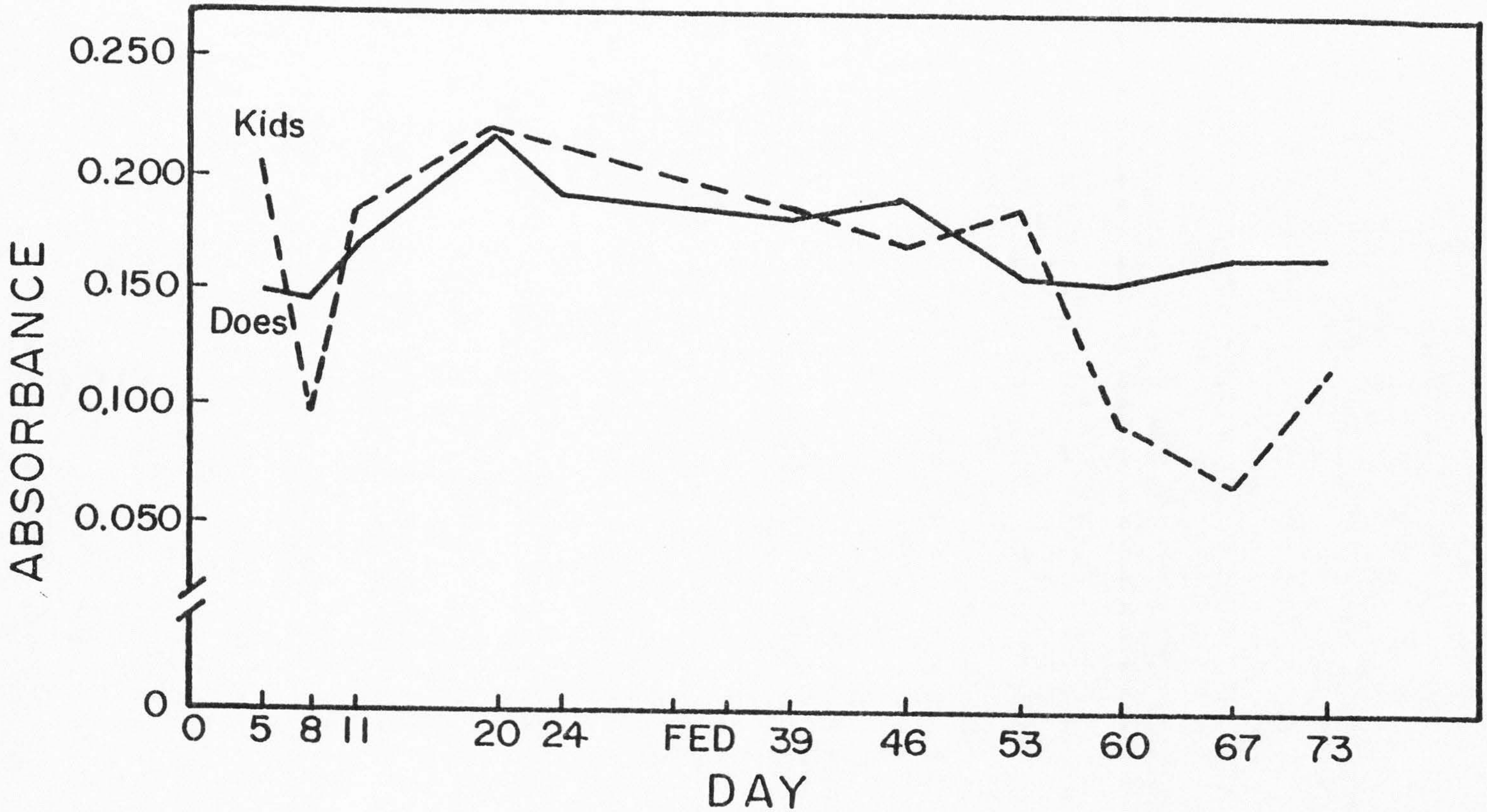


Figure 21. Tannin levels in the diets of esophageally fistulated kids and does browsing in blackbrush pastures from January 2 until March 17 of 1979.

levels in diets consumed by kids during the last three weeks of the study resulted from increased consumption of green grasses and forbs, and increased leaf:stem ratios.

The trend in crude protein levels for does and kids was similar to that of the leaf:stem ratio data (Figure 22, Appendix Table 36). Does initially consumed diets higher in crude protein, but toward the end of the study their diets contained lower levels of crude protein than diets of kids. Near the end of the study the elevated crude protein levels in the diets of kids resulted from increased leaf:stem ratios as well as higher levels of green grasses and forbs.

Kids consumed diets which were generally more digestible than those consumed by does (Figure 23, Appendix Table 37). Increased digestibilities on days 39 and 46 probably resulted from increased consumption of alfalfa. Averaged throughout the study, kids and does which browsed in the heavily stocked pasture consumed diets of 44.8 percent and 44.5 percent IVDMD, while kids and does which browsed in the lightly stocked pasture consumed diets of 44.6 percent and 42.2 percent IVDMD. Lower IVDMD of diets consumed by does that browsed in the lightly stocked pastures probably resulted from a higher proportion of older blackbrush twigs, and a lower consumption of green grasses and forbs.

Activity budgets. Statistical analysis of the activity budget data was influenced by the large number of degrees of freedom for the date X animals/intensity X class X fistulation error term, which resulted in extremely sensitive tests of interactions (Appendix

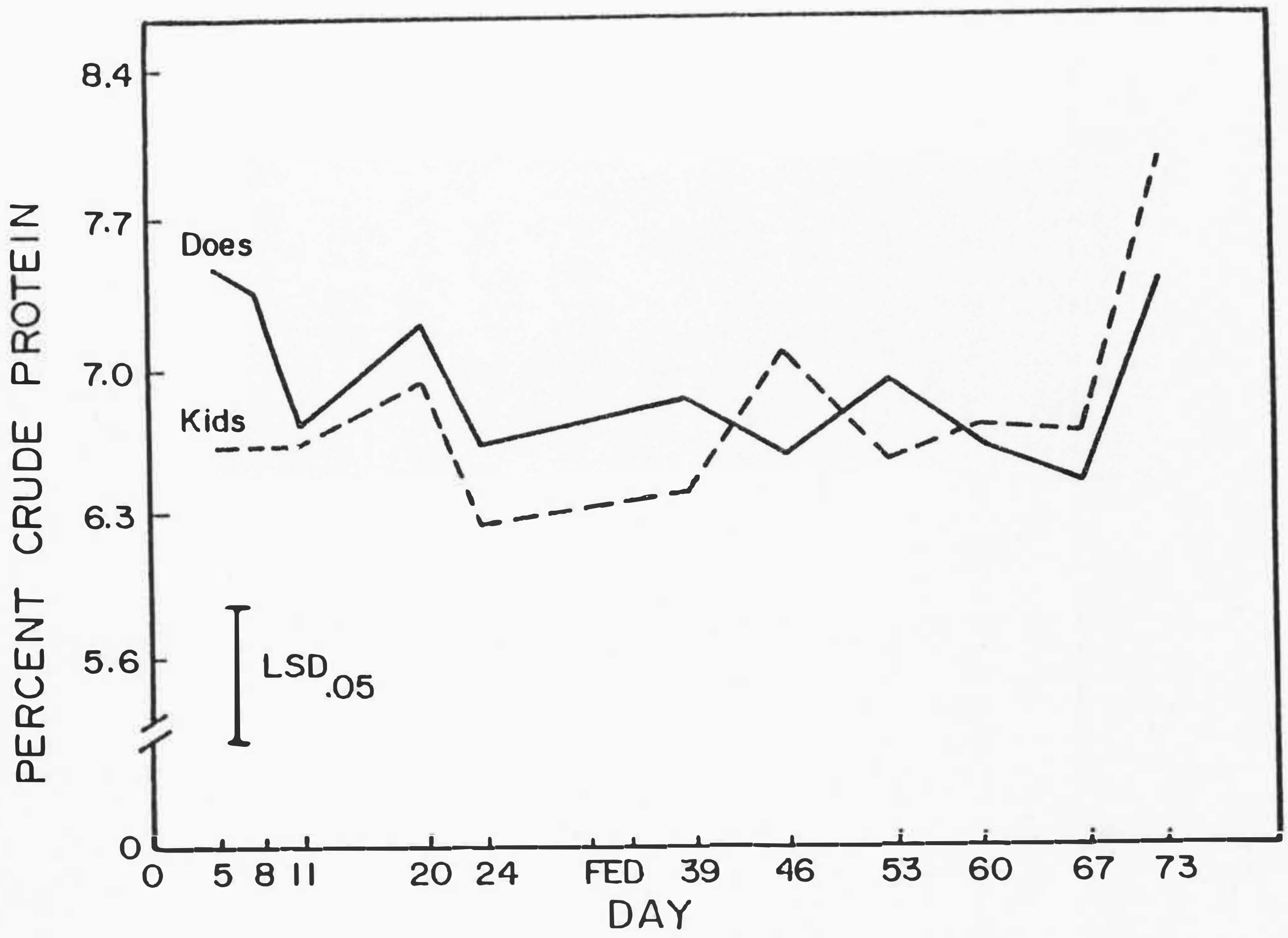


Figure 22. Percent crude protein in the diets of esophageally fistulated does and kids browsing in blackbrush pastures from January 2 until March 17 of 1979.

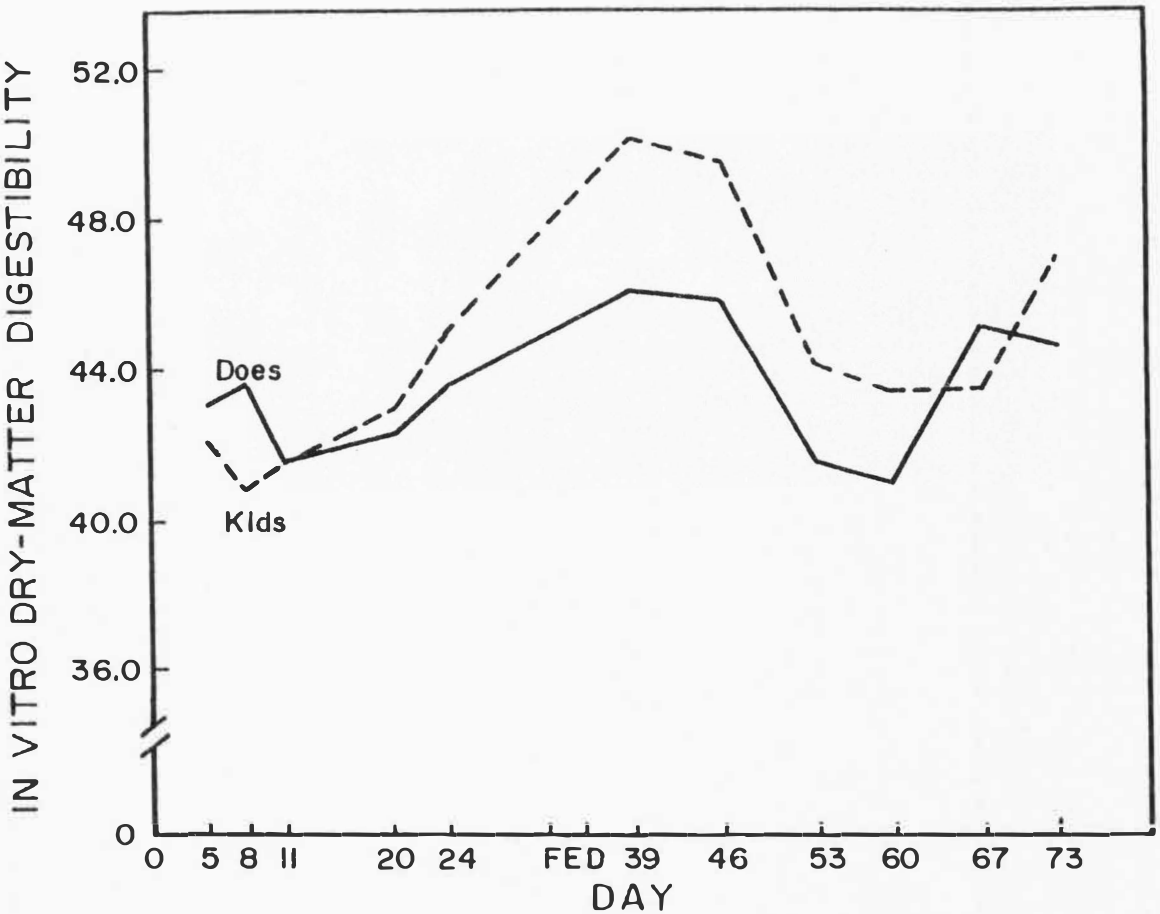


Figure 23. In vitro dry-matter digestibility of diets consumed by esophageally fistulated does and kids browsing in blackbrush pastures from January 2 until March 17 of 1979.

Table 38). Thus, trends that were quite similar for the three-way interactions were significantly different. To compensate, only the significant two-way interactions were considered.

The amount of time fistulated and nonfistulated goats spent browsing was similar; however, the interaction between age class and fistulation was significant. Fistulated and nonfistulated kids spent a similar amount of time browsing (60 percent versus 63 percent); however, fistulated does spent more time browsing than nonfistulated does (48 percent versus 41 percent). The reason fisulated kids spent less time browsing, and fistulated does spent more time browsing, than their nonfistulated counterparts was not apparent. This may have been a chance occurrence, since fistulated and nonfistulated goats reacted similarly in other respects.

Goats in the lightly stocked pasture spent more time browsing than those in the heavily stocked pasture (Figure 24). Perhaps the greater variety of plants available to goats in the lightly stocked pasture stimulated them to search more while browsing. Browsing time increased during the last three weeks of the study in both the heavily and lightly stocked pastures to nearly 80 percent, due to the appearance of green grasses and forbs.

The amount of time goats spent browsing generally increased during the season. Goats may undergo annual fluctuations in metabolism which affect foraging time. Moen (1978) indicated that white-tailed deer (*Odocoileus virginianus*) exhibited seasonal rhythms in metabolism and intake with lows during the winter months. Further research is necessary with goats concerning this phenomenon.

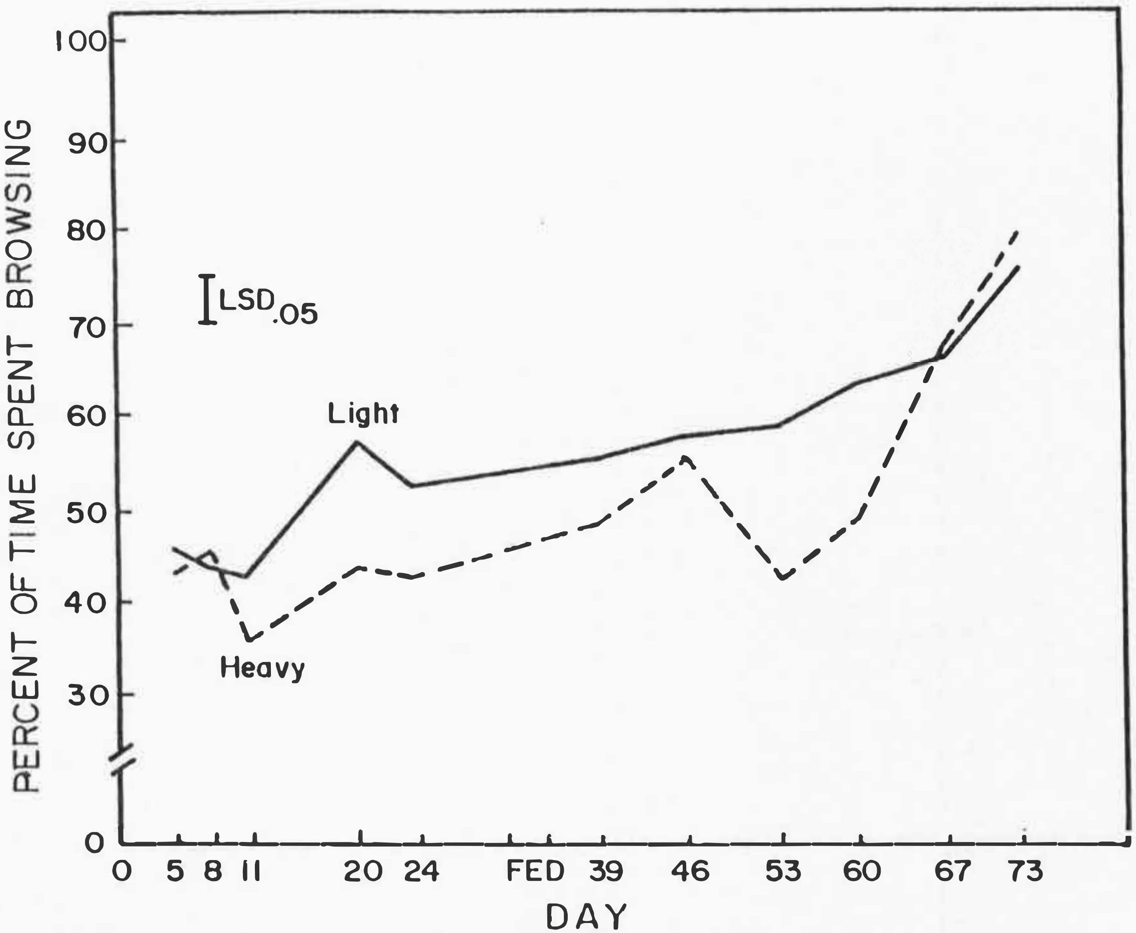


Figure 24. Percent of time between 8 a.m. and 5 p.m. that goats in lightly and heavily stocked blackbrush pastures spent browsing from January 2 until March 17 of 1979.

Kids spent more time browsing than does despite any social facilitation which may have occurred (McClymont 1967, Figure 25). During the latter part of the browsing period, however, the diets consumed by kids contained higher leaf:stem ratios, more crude protein, and higher IVDMD. Perhaps kids spent more time foraging later in the season as a result of being more selective (Figure 20), rather than a lack of experience; either would necessitate a greater time expenditure to meet daily intake requirements. Whether or not the nutrients and energy consumed by browsing longer were sufficient to compensate for the energy expended in foraging would be worth answering in future research.

Weights. Goats browsing in the heavily stocked pasture lost less weight than goats browsing in the lightly stocked pasture (Figure 26, Appendix Table 39). This response could probably be attributed to the higher nutrient content and digestibility of their diets, coupled with lesser time spent foraging.

The concepts of hedyphagia (food selection to minimize unpleasant and maximize pleasant olfactory and gustatory sensations) and euphagia (food selection to meet specific nutrient needs) are interesting to consider in this respect. Goats browsing in the heavily stocked pasture consumed diets higher in leaf:stem ratios, crude protein content, and in vitro dry-matter digestibility. Yet, when given a choice, goats preferred not to eat CSG, presumably because of high tannin levels. This provides additional evidence that, although animals (goats) may be innately euphagic, this is secondary to hedyphagia (Arnold and Dudzinski 1978).

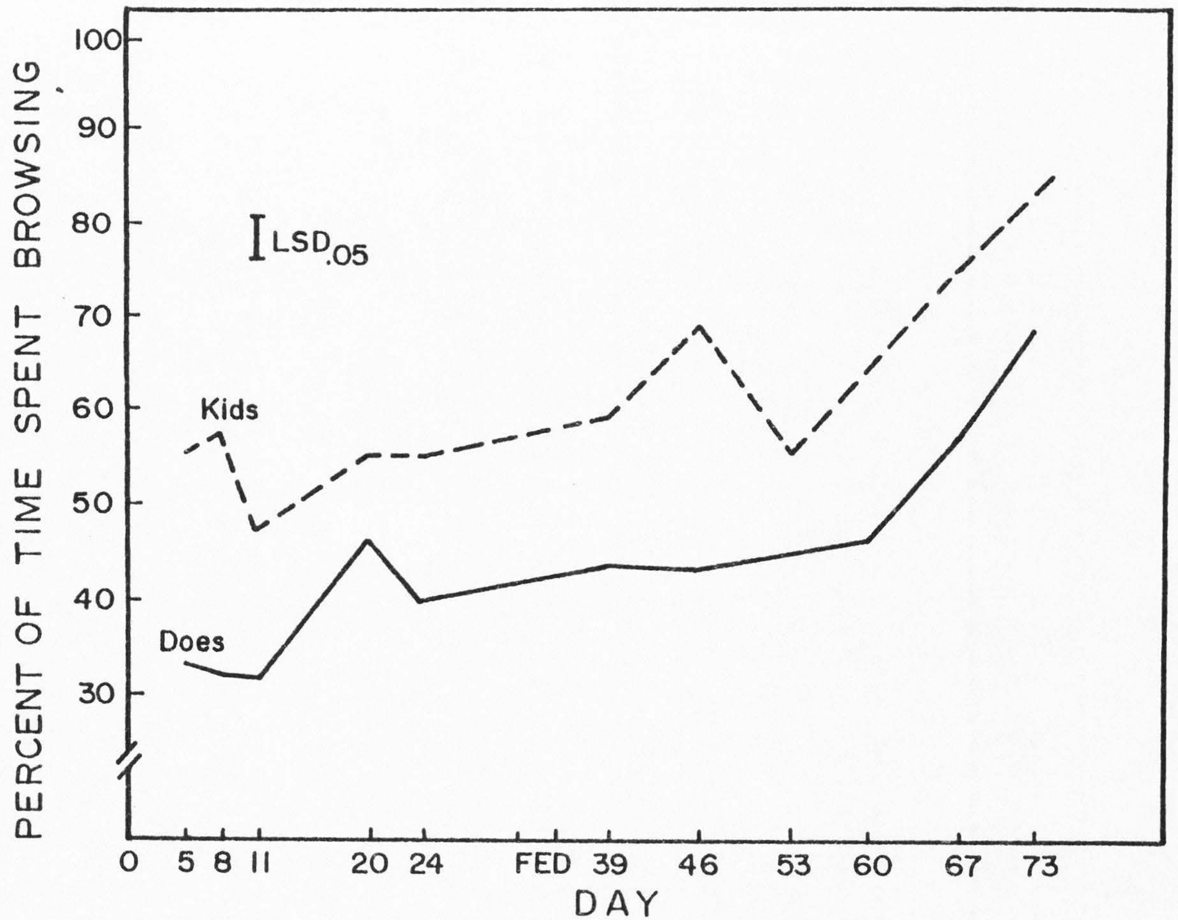


Figure 25. Percent of time between 8 a.m. and 5 p.m. that kids and does in blackbrush pastures spent browsing from January 2 until March 17 of 1979.

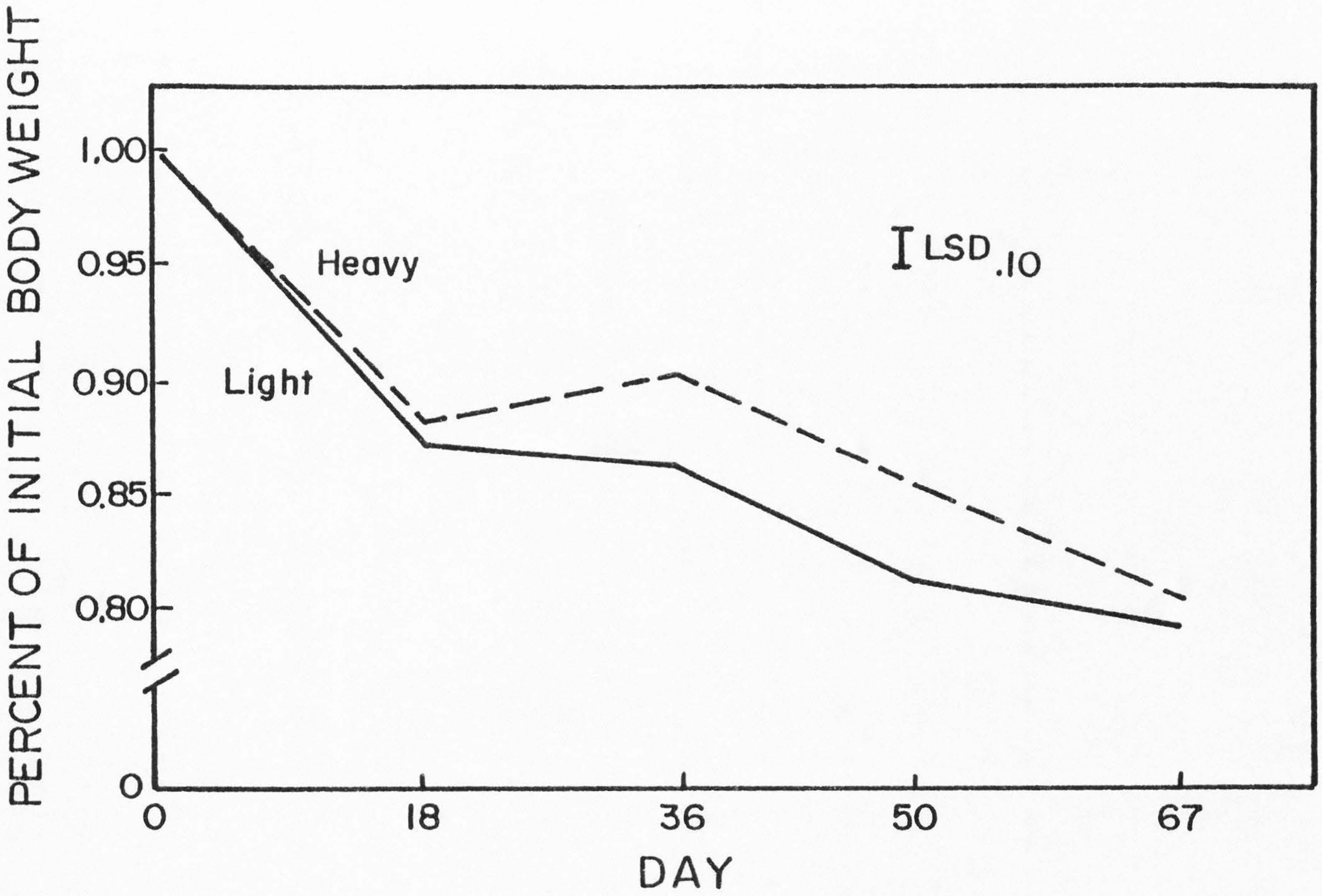


Figure 26. Percent body weight change for goats browsing in heavily and lightly stocked blackbrush pastures from January 2 until March 17 of 1979.

Kids lost more weight than does as the browsing season progressed (Figure 27). Apparently, the additional nutrients and energy consumed by kids did not compensate for their higher requirements and the increased amount of time, and presumably energy, spent foraging.

The stocking rate X age class X fistulation interaction was statistically significant. In the heavily stocked pasture, weight loss by fistulated and nonfistulated kids was similar, but fistulated does lost more weight than nonfistulated does. However, in the lightly stocked pasture, fistulated kids lost more weight than nonfistulated kids, while nonfistulated does lost more weight than fistulated does. These results may have been due to chance and the underlying causes are unknown.

Analysis of the weight response data for all pastures in 1979 indicated that does lost less weight than kids (Appendix Table 40), and the trend was similar to that in Figure 27. No statistically significant differences were noted among the three stocking levels. The weight loss trend, however, was moderately stocked < heavily stocked < lightly stocked.

Supplementation

Weights. A summary of the split-plot supplementation study during the winter of 1978 is presented in Figure 28. Unsupplemented goats lost more weight than supplemented goats as the season progressed (Appendix Table 41). However, the percent of body weight lost by unsupplemented goats was low.

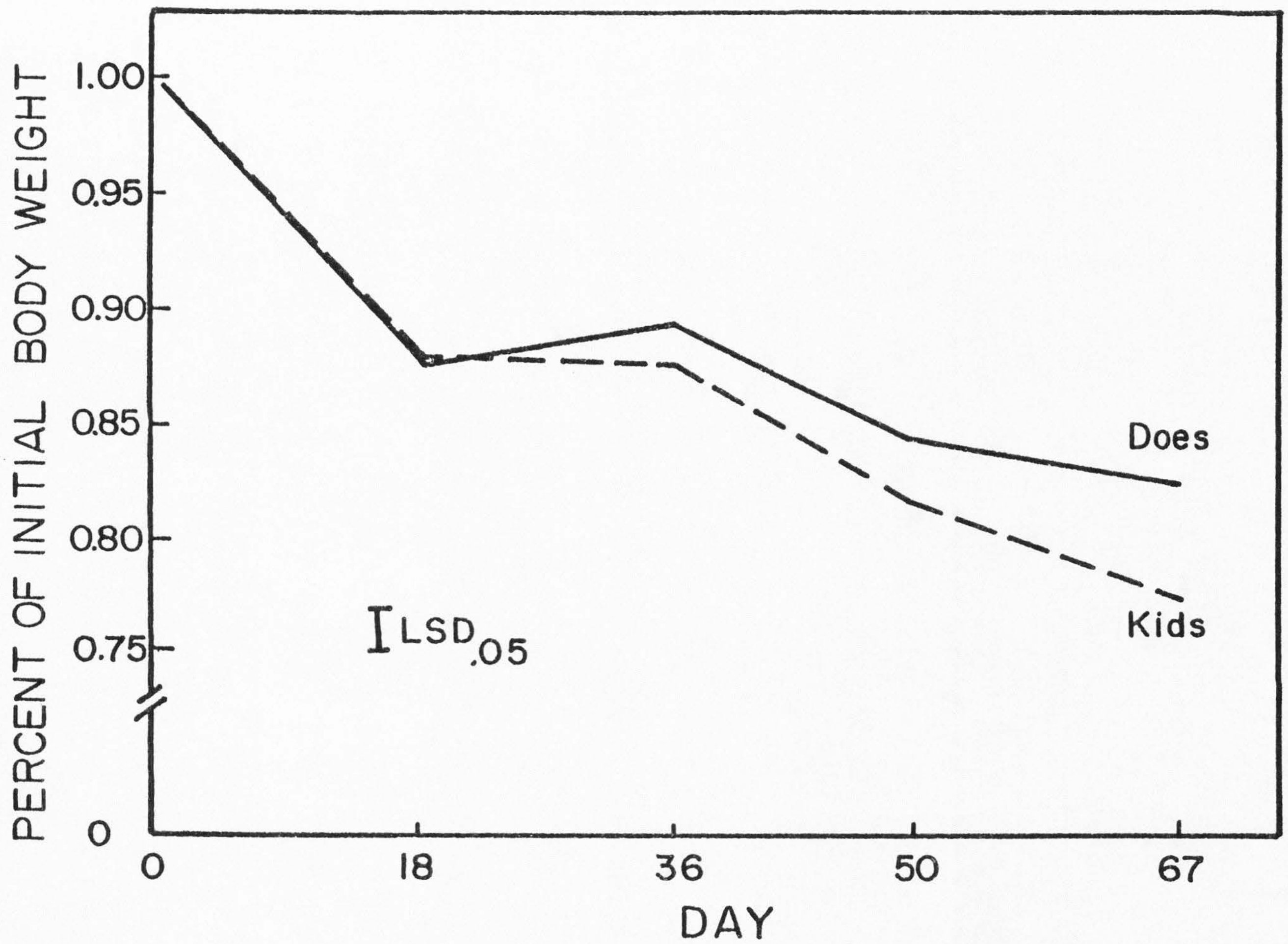


Figure 27. Percent body weight change for does and kids browsing in blackbrush pastures from January 2 until March 17 of 1979.

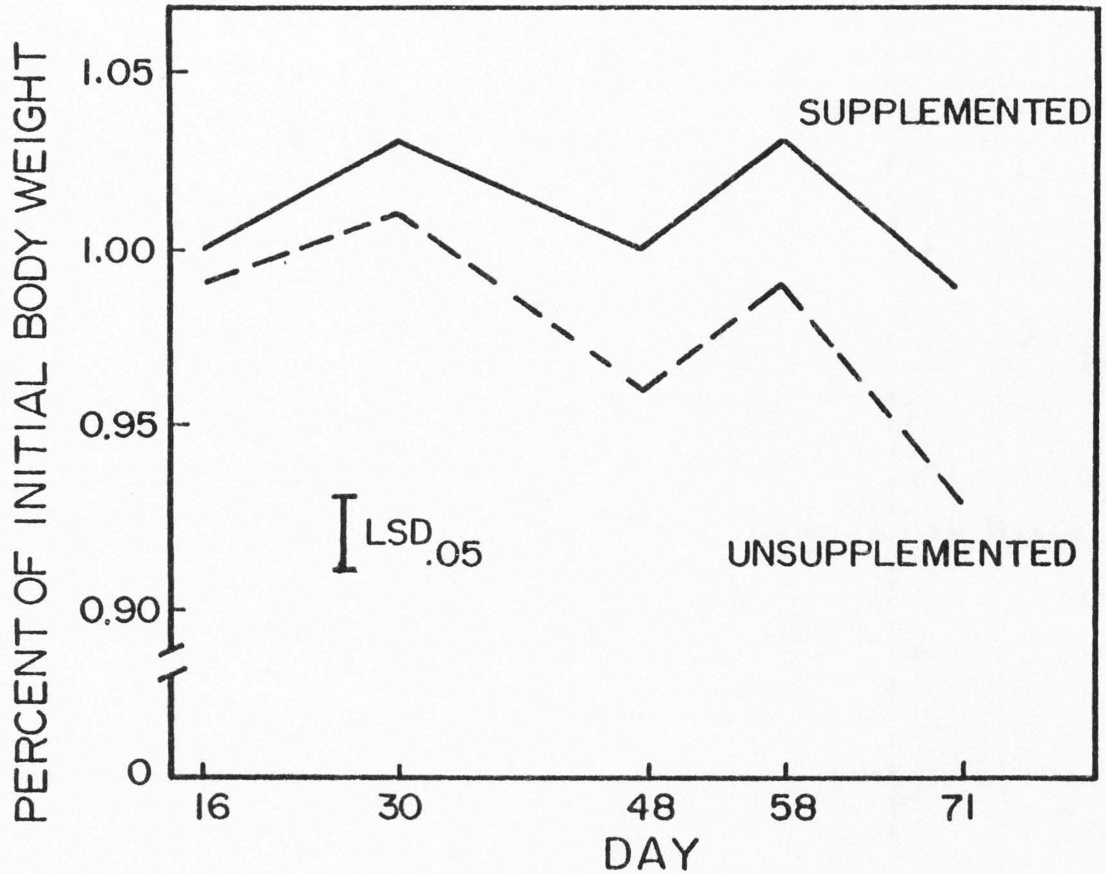


Figure 28. Percent body weight change for supplemented and unsupplemented goats browsing in blackbrush pastures from December 29 until March 11 of 1978.

The difference in weight response by the same goats in 1979 and 1978 was interesting. Does browsing in blackbrush pastures in 1979 (Figure 27) lost 18 percent of body weight, while unsupplemented does browsing in blackbrush pastures in 1978 lost 7 percent of body weight. A possible explanation for the difference in weight response is that in 1978 the does had just arrived from Texas and were accustomed to foraging on rangelands. For nine months prior to the 1979 browsing season, however, these does were penned and fed alfalfa hay. As a result, in 1979 the does weighed more (37 kg in 1979 versus 33 kg in 1978) and were in a higher body condition, hence they were more prone to weight loss when moved onto the range.

Response of Cattle to Blackbrush Manipulation by Goats

Comparison of goat-browsed and unbrowsed pastures

Diets. Hand-plucked blackbrush samples that simulated twigs consumed by cattle browsing in blackbrush pastures were analyzed for percent CSG (Figure 29), tannin levels (Figure 30), crude protein levels (Figure 31), and IVDMD (Figure 32, Appendix Tables 42-45). A positive relationship existed between percent CSG and tannin levels (r^2 = 0.78), crude protein levels (r^2 = 0.70), and IVDMD (r^2 = 0.65). Unaccounted variability due to plants, twig age, and twig location affected these relationships, lowing the coefficients of determination.

Cattle in previously unbrowsed pastures (control) consumed less CSG than cattle in previously browsed pastures (heavy, moderate,

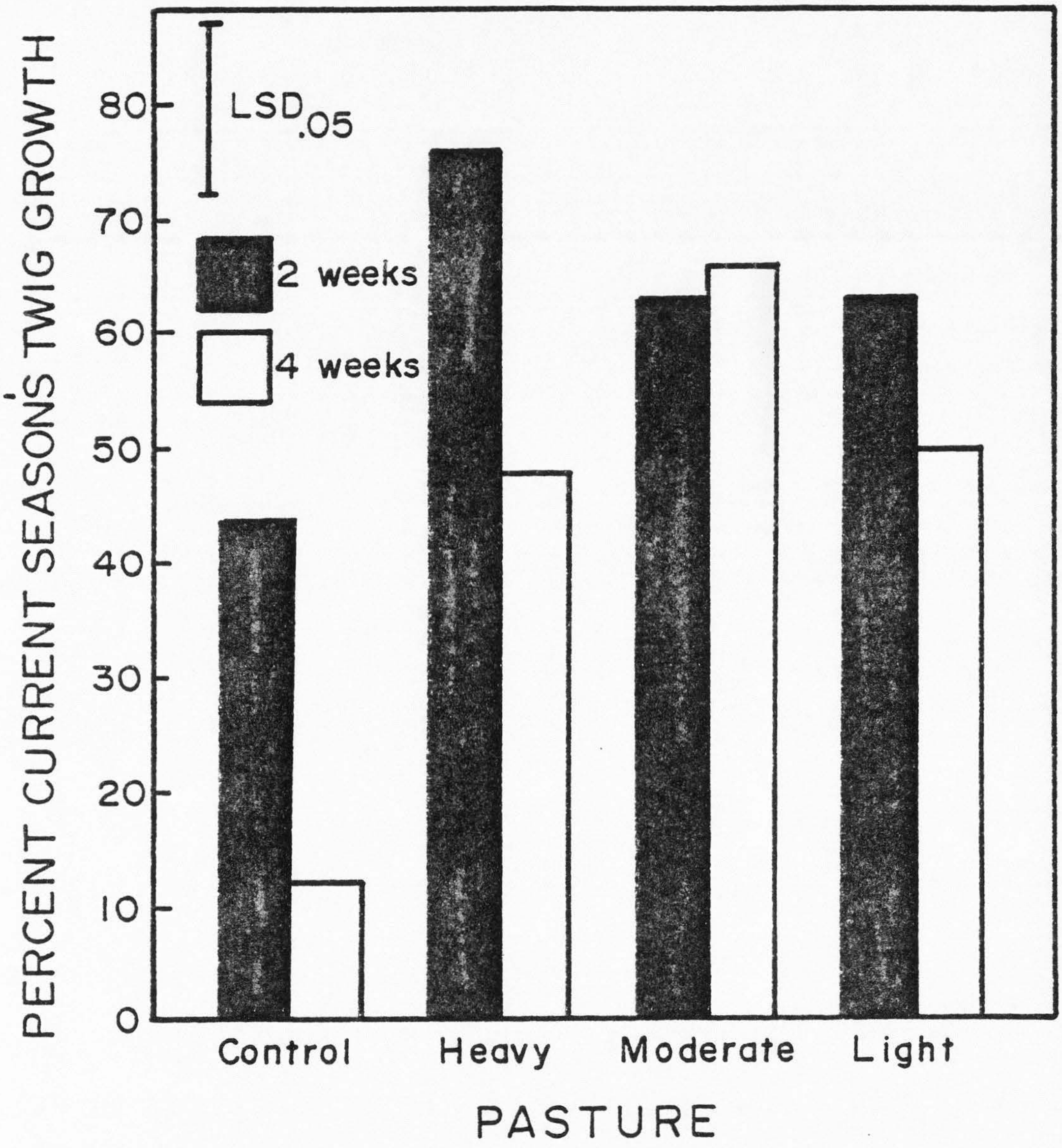


Figure 29. Percent current season's twig growth in the simulated diets (hand-plucked) of cattle browsing blackbrush pastures during October of 1979.

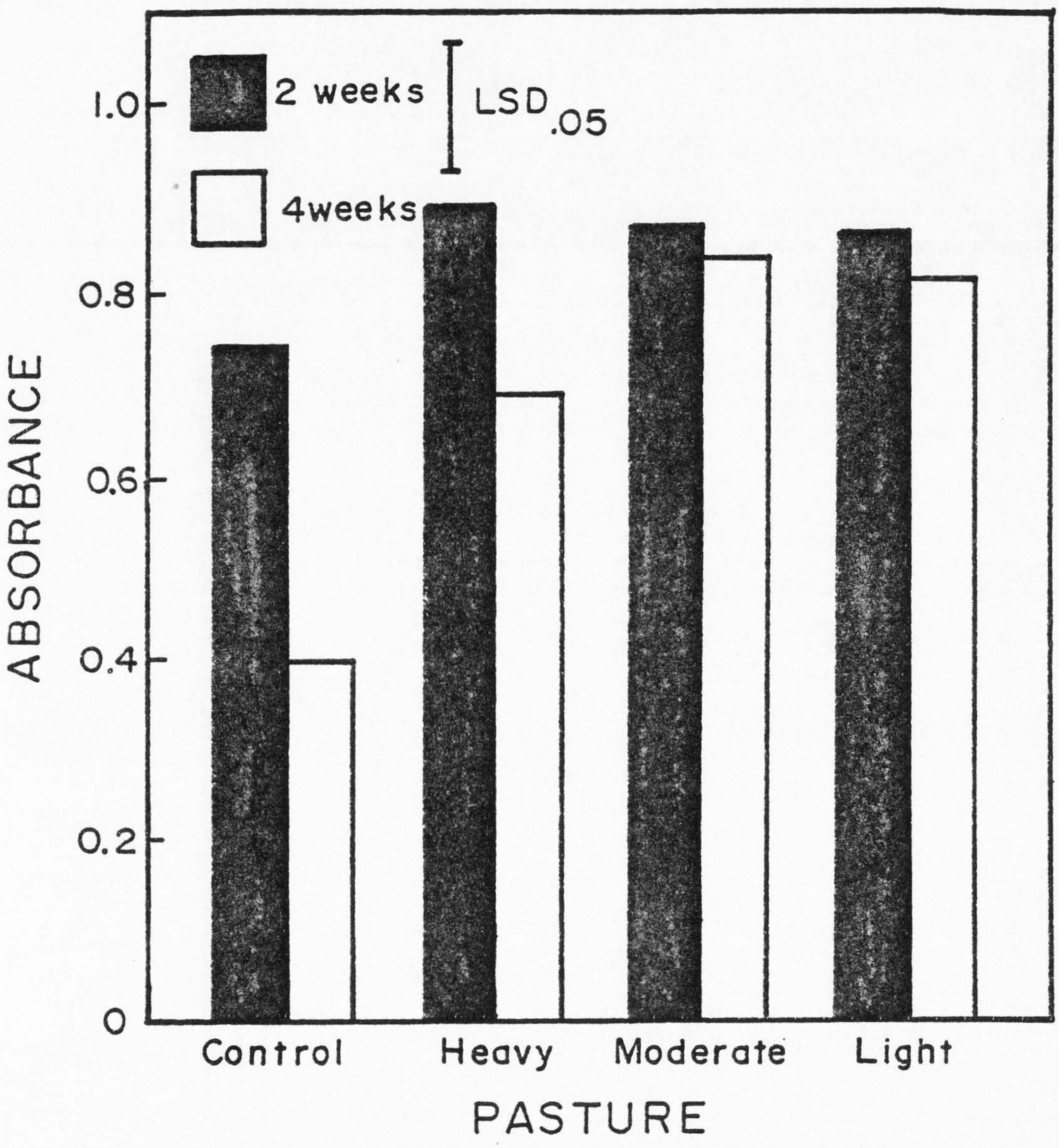


Figure 30. Tannin levels in the simulated diets (hand-plucked) of cattle browsing blackbrush pastures during October of 1979.

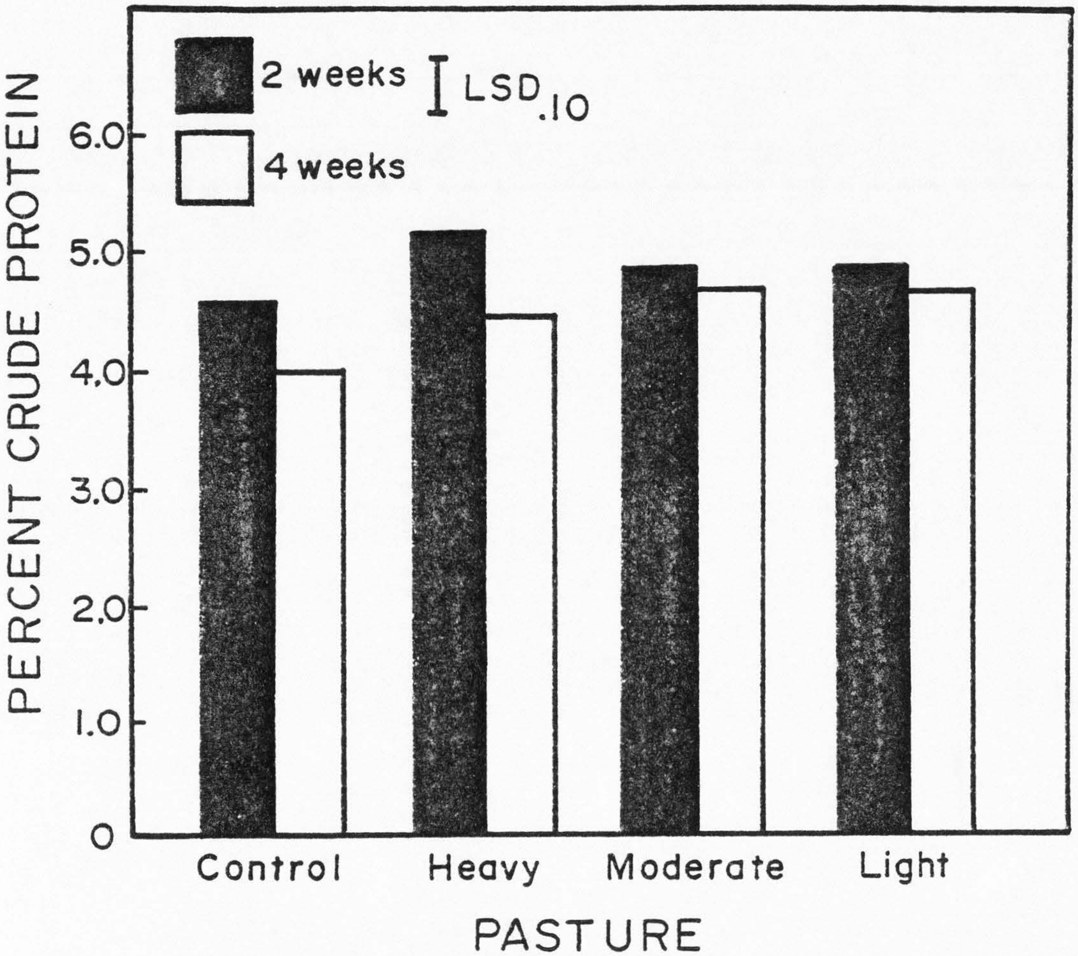


Figure 31. Percent crude protein in the simulated diets (hand-plucked) of cattle browsing blackbrush pastures during October of 1979.

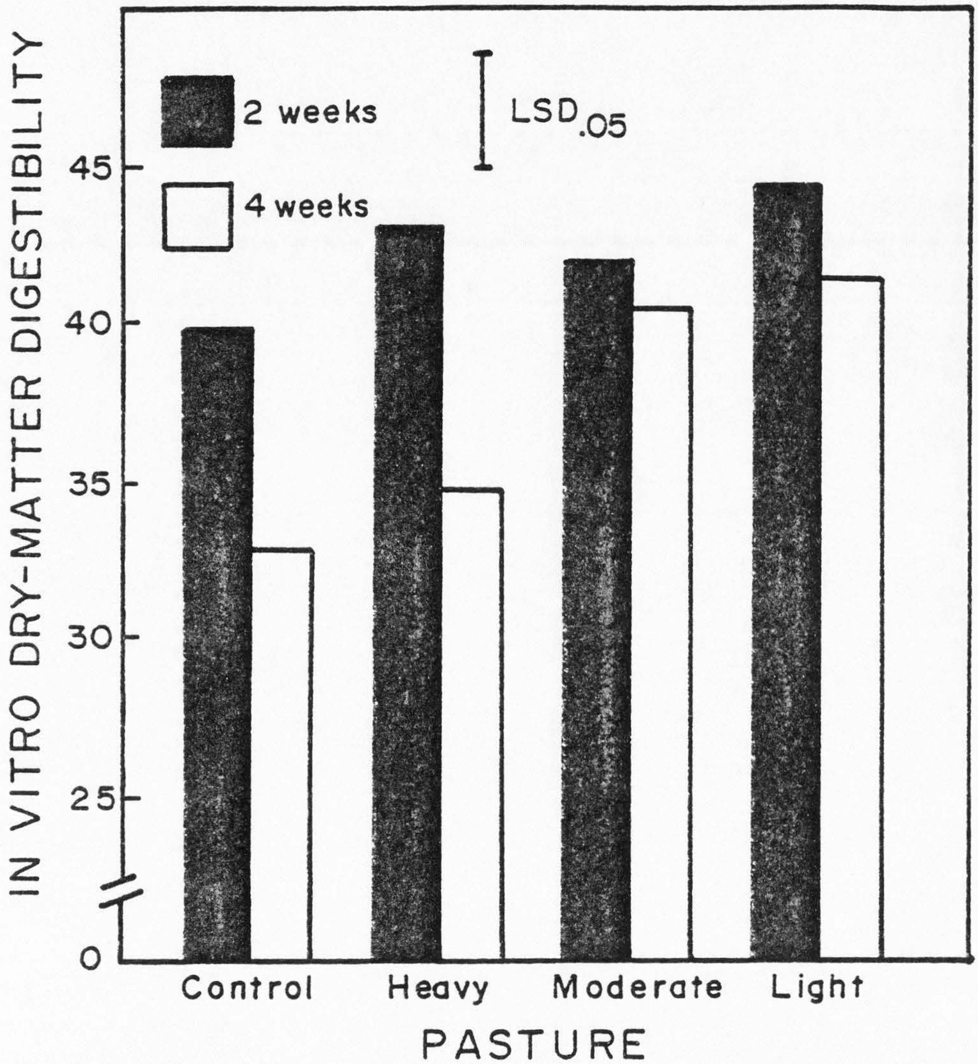


Figure 32. In vitro dry-matter digestibility of the simulated diets (hand-plucked) of cattle browsing in blackbrush pastures during October of 1979.

light) due to the woody nature of unbrowsed plants. Cattle browsing in the heavily stocked pasture consumed the greatest quantity of CSG due to the high twig production in that pasture resulting from previous goat browsing and abundant moisture during 1979. The percent CSG consumed by cattle browsing in the control and heavily stocked pastures declined during October, however, due to the heavy stocking intensities (Table 7). The percent CSG consumed by cattle browsing in the moderately and lightly stocked pastures remained constant due to the lower stocking intensities. Cattle tended to prefer basal branches in all blackbrush pastures, and as the percent CSG declined, the levels of crude protein, IVDMD, and tannins also declined.

Activity budgets. Cattle spent less time browsing in early October than later in the month (Figure 33, Appendix Table 46). The increased time spent browsing by animals in the control and heavily stocked pastures probably resulted from decreased forage availability as utilization levels increased (Table 7, Arnold 1964). Heifers browsing in the lightly stocked pasture exhibited a similar trend in foraging time to heifers in the control and heavily stocked pasture, while heifers in the moderately stocked pasture spent the least time browsing. The reasons for the responses of heifers in the lightly and moderately stocked pastures are unclear.

Weights. Cattle browsing in blackbrush pastures were supplemented with 36 percent protein blocks. No statistically significant differences in weight responses were recorded for heifers

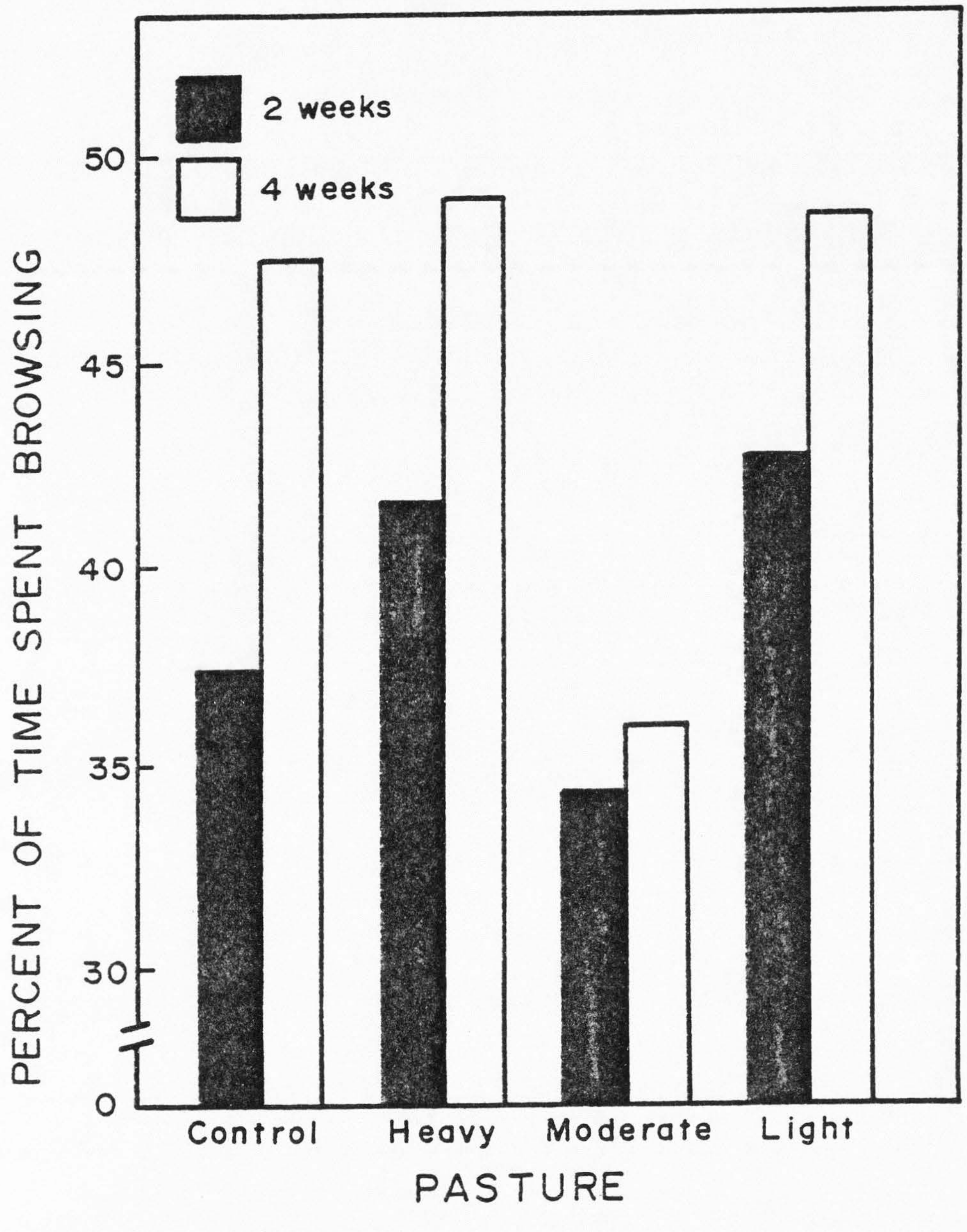


Figure 33. Percent of time between 8 a.m. and 7 p.m. that cattle in blackbrush pastures spent browsing during October of 1979.

browsing in previously unbrowsed versus previously browsed pastures (Appendix Table 47). However, the average heifer gained 0.64 $kg \cdot day^{-1}$ during the first two weeks of the study and lost 0.01 $kg \cdot day^{-1}$ during the last two weeks of the study.

Statistically significant differences in consumption of protein block were recorded for heifers in previously browsed versus previously unbrowsed pastures (Appendix Table 48). Animals in previously unbrowsed pastures ate more protein block (Figure 34). Block consumption varied among pastures which were previously browsed, however, no trends were apparent. Heifers in all pastures increased consumption of protein block throughout the browsing period. Over the course of the study, the average heifer (268 kg) in previously browsed versus previously unbrowsed pastures consumed 0.94 kg versus 1.77 kg of protein block daily, respectively.

The low crude protein levels and woody nature of twigs in previously unbrowsed pastures probably decreased the digestibility of diets consumed there (Table 12), and may have contributed to the increased consumption of protein block by heifers browsing in those pastures. The assumption is that crude protein levels in the blackbrush diets were low for effective rumen function, and additional protein from the blocks improved the digestibility and, presumably, intake of the twigs (van Glyswyk 1970).

Tannins decrease digestibility (Donnelly and Anthony 1970, Nastis and Malechek 1981, Donnelly and Hawkins 1955, referenced in McLeod 1974), apparently by reducing nitrogen and carbohydrate degradation in the rumen and increasing fecal nitrogen excretion.

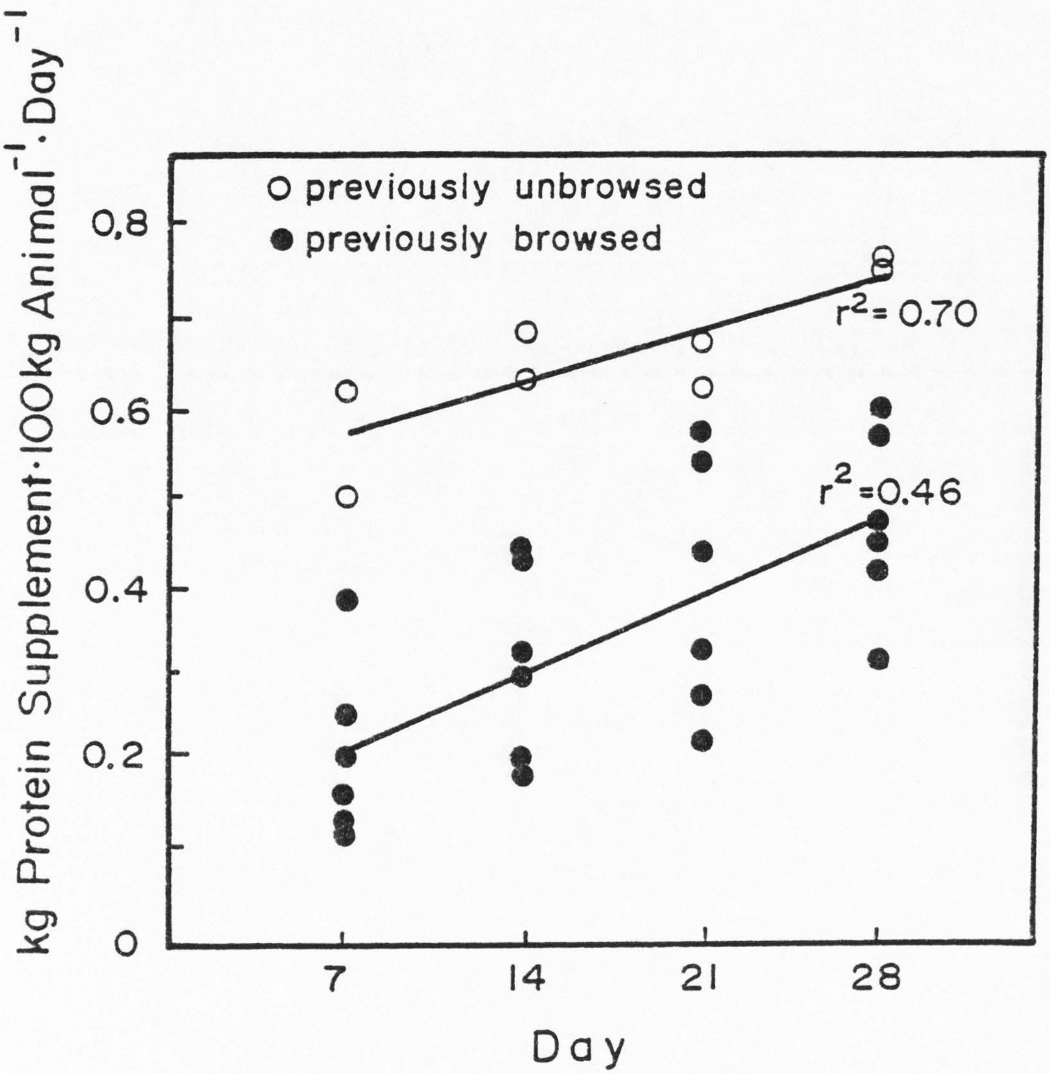


Figure 34. Quantity of 36 percent protein block consumed by cattle browsing in blackbrush pasture during October of 1979.

Lignins reduce the availability of carbohydrates and proteins in a similar manner to tannins (Swain 1979), however, lignins probably decrease digestibility more than do tannins. Burns et al. (1972), for example, found that cattle were better able to adapt to increased tannin levels than increased fiber. Van Soest and McCammon-Feldman (1980) indicated that microbial adaptation to tannins may occur, but research is necessary on this subject.

The underlying question regarding differences in protein block consumption is whether heifers in the previously unbrowsed pasture consumed more protein block due to hedyphagic (palatability) or euphagic (improved rumen function) motivation. If increased consumption were due strictly to palatability, cattle browsing in the heavily stocked pastures should have consumed the most protein block, due to the low palatability of CSG produced by terminal branches. The fact that heifers in the previously unbrowsed pastures consumed the most protein block indicates that the response may be physiologically related to intake; however, research is needed in this area.

From a practical standpoint, protein supplementation is required to prevent weight loss, but some level of weight loss may be acceptable without supplementation. For example, Pinney et al. (1972) studied the effects of protein supplementation (60 percent, 120 percent, and 220 percent of recommended allowances) on lifetime production of beef cows. The cows that received the low level of supplementation lived longer and produced more calves of greater weaning weights than cows that recieved higher levels of supplementation.

Prior browsing apparently reduced the need for supplementation by increasing the nutrient content and digestibility of blackbrush twigs. Further research is necessary, however, to determine protein supplementation levels for cattle on previously unbrowsed versus browsed blackbrush rangelands.

SUMMARY

The objective of this research was to investigate the use of goats as biological manipulators of blackbrush to improve these rangelands for cattle. Winter goat browsing was employed to stimulate spring production of current season's twigs. The results of this research lead to the following conclusions:

1. Winter goat browsing stimulated current season's twig production by blackbrush plants, while rest after one or more years of browsing resulted in decreased twig production. Blackbrush plants were able to withstand repeated, heavy removal of CSG for at least four years without decreases in productivity or apparent losses of vigor. Terminal branches produced more CSG than basal branches on browsed plants, and plants growing on deep soils produced more CSG than plants growing on shallow soils.

2. Current season's twigs were higher in crude protein and phosphorus, and more digestible (in vitro) than older twigs. Twigs from basal branches were higher in crude protein and more digestible than those from terminal branches, and current season's twigs from blackbrush plants growing on deep soils were higher in crude protein and phosphorus, than twigs from plants growing on shallow soils.

3. Current season's twigs were higher in tannins than older twigs, and twigs from terminal branches were higher in tannins than twigs from basal branches. With rest from browsing, tannins

declined, due primarily to a decrease in the proportion of current season's to older growth.

4. Due primarily to the abundance of CSG, goats in the heavily stocked pasture consumed diets with higher leaf:stem ratios, and more crude protein, IVDMD, and tannins than goats in the lightly stocked pasture. Goats in the heavily stocked pasture spent less time browsing and lost less weight than goats in the lightly stocked pasture.

5. Does initially consumed diets higher in leaf:stem ratios and crude protein than kids, but kids later consumed diets higher in these constituents. Kids consumed diets higher in IVDMD than does; however, kids spent more time browsing and lost more weight than does.

6. Supplementation with protein and energy allowed goats to maintain body weight during the winter.

7. Cattle browsing on previously browsed versus previously unbrowsed pastures consumed higher levels of CSG. The CSG was higher in crude protein, IVDMD, and tannins than older growth.

8. No statistically significant differences in weight responses were recorded for cattle browsing in pastures which were, and were not, previously browsed by goats. However, heifers in previously unbrowsed pastures consumed nearly twice as much protein supplement as heifers in previously browsed pastures.

CONCLUSIONS AND RECOMMENDATIONS

Conclusions and recommendations stemming from this research relate to management and research. Specific recommendations for future management are:

1. Increase stocking intensities on blackbrush dominated rangelands to about 1.8 animal-unit-months$\cdot$ha^{-1}. This will require more intensive management, with increased fencing and water development. Water development and fencing are critical to proper use of blackbrush rangelands. Simply increasing (or decreasing) stocking intensities will not improve range use patterns if animals are allowed to water at stream bottoms or other areas where preferred grasses and forbs are more abundant. Blackbrush rangelands are best utilized by more intensive browsing of smaller areas.

2. Browsing systems should be established that employ heavy browsing followed by one or two years rest from browsing, depending on blackbrush twig production. Rest from browsing allows blackbrush plants to accumulate more twigs which are lower in tannin levels, and therefore more palatable. The primary purpose of rest is to allow an accumulation of palatable forage for consumption by livestock, rather than to benefit the plants, since blackbrush is apparently capable of withstanding heavy winter twig removal.

3. Animals browsing on blackbrush rangelands should be supplemented with protein to improve rumen function which will

diminish weight loss. Recommendations on specific timing and amounts can be made only after further research on this question.

4. Though not currently feasible economically, in the future goats may be used in conjunction with cattle on blackbrush rangelands. For the present, however, cattle are capable of manipulating and utilizing these rangelands.

Specific recommendations for future research relate to applied and basic studies. Recommendations for applied research are:

1. Determine stocking intensities and protein supplementation levels necessary for acceptable levels of performance by cattle browsing blackbrush rangelands during the winter.

2. Browsing system research is necessary with cattle and goats, comparing blackbrush utilization when these species are browsed singly and in combination.

Recommendations for basic research, which could be conducted in conjunction with the applied research, are:

1. Conduct research relative to plant-antiherbivore theory to determine:

a) Physiological and chemical responses of blackbrush to browsing relative to Rhoades (1979) hypotheses.

b) The relationship between spinescence and tannin levels for browsed blackbrush plants, i.e, are tannin levels lower in spinescent plants due to their protective growth form?

c) Tannin allocation to basal versus terminal branches under various branch removal regimes.

2. Conduct research relative to plant-animal interactions to determine:

a) The relationships among branch location, spinescence, woodiness, and tannin levels as they affect palatability.

b) The effects of tannins on in vitro dry-matter digestibility techniques for predicting in vivo digestibility.

c) The reason(s) for the greater intake of protein supplement by heifers in previously unbrowsed versus previously browsed blackbrush pastures, i.e., was the response due to hedyphagic behavior, or physiologically related to rumen function?

d) Whether kids spent more time browsing due to increased selection, decreased intake due to inexperience, or both.

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APPENDIX

Table 15. Analysis of variance for the 1978 goat utilization data.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Replication	1	560.71	<1	NS
Intensity	2	262,915.80	98.31	0.01002
Error A	2	2,674.22	-	--
Location	1	16,598.01	5.30	0.10485
Location X Intensity	2	1,569.39	<1	NS
Error B	3	3,133.73	-	--

Table 16. Analysis of variance for the 1979 goat utilization data.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Replication	1	2,972.57	<1	NS
Intensity	2	143,825.30	25.80	0.03665
Error A	2	5,575.10	-	--
Location	1	30,048.71	15.20	0.02994
Location X Intensity	2	14,547.45	7.36	0.06965
Location X Heavy vs Moderate, Light	1	29,090.58	14.72	0.03122
Error B	3	1,976.32	-	--

Table 17. Analysis of variance for the 1979 cattle utilization data.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Replication	1	2,440.36	3.69	NS
Intensity	3	243,611.50	368.17	0.00031
Error A	3	661.68	-	--
Location	1	141.78	<1	NS
Location X Intensity	3	7,210.01	3.83	0.11353
Location X Control, Heavy vs Moderate, Light	1	16,924.73	9.00	0.03994
Error B	4	1,880.71	-	--

Table 18. Analysis of variance for current season's twig production by blackbrush plants browsed at four stocking intensities in 1978.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Replication	1	15,365,420	1.67	NS
Intensity	3	25,252,600	2.74	NS
Heavy vs Moderate, Light, Control	1	69,153,325	7.51	0.07130
Error A	3	9,206,684	-	--
Location	1	75,039,180	10.47	0.03181
Location X Intensity	3	16,254,320	2.27	NS
Error B	4	7,167,836	-	--

Table 19. Analysis of variance for current season's twig production by blackbrush plants browsed at four stocking intensities in 1979.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Replication	1	5,163,461	<1	NS
Intensity	3	12,820,070	2.08	NS
Heavy vs Moderate, Light, Control	1	32,788,139	5.33	0.10411
Error A	3	6,148,905	-	--
Location	1	81,504,310	16.99	0.01458
Location X Intensity	3	8,144,273	1.70	NS
Error B	4	4,795,945	-	--

Table 20. Analysis of variance for current season's twig production by the terminal and basal branches of blackbrush plants growing on deep and shallow soils in 1977. Plants were browsed and rested from browsing.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Years	4	356,284	4.99	0.00182
Soil	1	547,998	7.68	0.00781
Years X Soil	4	19,793	<1	NS
Plants/Years X Soil	50	71,335	-	--
Location	1	4,429,875	73.51	<0.00000
Location X Years	4	103,395	1.72	NS
Location X Soil	1	829,199	13.76	0.00052
Location X Years X Soil	4	33,394	<1	NS
Location X Plants/Years X Soil	50	60,266	-	--

Table 21. Analysis of variance for current season's twig production by the terminal and basal branches of blackbrush plants growing on deep and shallow soils in 1978. Plants were browsed and rested from browsing.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Years	4	3,280,608	5.25	0.00132
Soil	1	13,055,170	20.88	0.00003
Years X Soil	4	1,423,053	2.28	NS
Plants/Years X Soil	50	625,392	-	--
Location	1	55,837,451	93.60	<0.00000
Location X Years	4	2,862,799	4.80	0.00235
Location X Soil	1	6,077,298	10.19	0.00245
Location X Years X Soil	4	1,434,164	2.40	NS
Location X Plants/Years X Soil	50	596,546	-	--

Table 22. Analysis of variance for current season's twig production by the terminal and basal branches of blackbrush plants growing on deep and shallow soils in 1979. Plants were browsed and rested from browsing.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Years	4	4,905,801	8.64	0.00002
Soil	1	7,369,530	12.97	0.00074
Years X Soil	4	1,201,426	2.11	NS
Plants/Years X Soil	49	568,054	-	--
Location	1	45,814,892	77.02	<0.00000
Location X Years	4	4,079,936	6.86	0.00020
Location X Soil	1	7,145,652	12.01	0.00116
Location X Years X Soil	4	1,171,774	1.97	NS
Location X Plants/Years X Soil	46	594,866	-	--

Table 23. Analysis of variance for current season's twig production by the terminal and basal branches of blackbrush plants growing on deep and shallow soils in 1980. Plants were browsed and rested from browsing.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Years	5	3,014,254	9.49	<0.00000
Soil	1	7,610,462	23.95	0.00001
Years X Soil	5	526,522	1.66	NS
Plants/Years X Soil	59	317,717	-	--
Location	1	31,538,098	102.66	<0.00000
Location X Years	5	1,956,721	6.33	0.00009
Location X Soil	1	4,872,140	15.77	0.00020
Location X Years X Soil	5	531,696	1.72	NS
Location X Plants/Years X Soil	59	309,010	-	--

Table 24. Analysis of variance for the percent crude protein in current season's and older twigs from the terminal branches of blackbrush plants growing on deep and shallow soils.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Twig	1	108.2288	34.60	0.00981
Soil	1	14.2444	4.55	0.12256
Year	1	60.6378	19.38	0.02173
Twig X Soil	1	1.9256	<1	NS
Error	3	3.1282	-	--

Table 25. Analysis of variance for the percent phosphorus in current season's and older twigs from the terminal branches of blackbrush plants growing on deep and shallow soils.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Twig	1	0.018528	6.92	0.07827
Soil	1	0.014028	5.24	0.10604
Year	1	0.028800	10.76	0.04643
Twig X Soil	1	0.000013	<1	NS
Error	3	0.002677	-	--

Table 26. Analysis of variance for the in vitro dry-matter digestibility of current season's and older twigs from the terminal branches of blackbrush plants growing on deep and shallow soils.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Twig	1	2916.86	31.62	0.01112
Soil	1	5.85	<1	NS
Year	1	231.58	2.51	NS
Twig X Soil	1	2.02	<1	NS
Error	3	92.25	-	--

Table 27. Analysis of variance for the percent crude protein in terminal and basal twigs from blackbrush branches.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Plants	5	1.20042	3.94	0.07922
Location	1	1.22402	4.02	0.10129
Error	5	0.30447	-	--

Table 28. Analysis of variance for the in vitro-dry matter digestibility of terminal and basal twigs from blackbrush branches.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Plants	5	16.57948	1.91	NS
Location	1	56.18160	6.47	0.05166
Error	5	8.68279	-	--

Table 29. Analysis of variance for tannin levels in twigs growing on the terminal and basal branches of blackbrush plants growing on deep and shallow soils in 1980. Plants were browsed and rested from browsing.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Years	5	0.706569	9.45	0.00004
Soil	1	0.182614	2.44	NS
Years X Soil	5	0.044380	<1	NS
Plants/Years X Soil	24	0.074745	-	--
Location	1	0.407895	60.90	<0.00000
Location X Years	5	0.088544	13.22	<0.00000
Location X Soil	1	0.034534	5.16	0.03242
Location X Years X Soil	5	0.015621	2.33	NS
Location X Plants/Years X Soil	24	0.006698	-	--

Table 30. Analysis of variance for tannin levels in the leaves and twigs of basal and terminal blackbrush branches.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Plants	5	0.072461	6.12	0.00279
Location	1	0.347821	29.37	0.00007
Part	1	0.499800	42.20	0.00001
Location X Part	1	0.219240	18.51	0.00063
Error	15	0.011844	-	--

Table 31. Analysis of variance for the percent blackbrush in the diets of esophageally fistulated does and kids browsing in heavily and lightly stocked pastures from January 2 until March 17 of 1979.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Intensity	1	0.014903	4.03	0.07952
Class	1	0.022494	6.09	0.03889
Intensity X Class	1	0.008608	2.33	NS
Animals/Intensity X Class	8	0.003696	-	--
Date	10	0.006548	<1	NS
Date X Intensity	10	0.009175	1.30	NS
Date X Class	10	0.003294	<1	NS
Date X Intensity X Class	10	0.002843	<1	NS
Date X Animals/Intensity X Class	45	0.007047	-	--

Table 32. Analysis of variance for leaf:stem ratios for blackbrush in the diets of esophageally fistulated does and kids browsing in heavily and lightly stocked pastures from January 2 until March 17 of 1979.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Intensity	1	0.024620	2.14	NS
Class	1	0.000457	<1	NS
Intensity X Class	1	0.000902	<1	NS
Animals/Intensity X Class	8	0.011531	-	--
Date	10	0.016343	2.12	0.04235
Date X Intensity	10	0.037236	4.83	0.00010
Date X Class	10	0.012520	1.62	0.13034
Date X Intensity X Class	10	0.009205	1.19	NS
Date X Animals/Intensity X Class	45	0.007706	-	--

Table 33. Analysis of variance for tannin levels in terminal and basal twigs of masticated and unmasticated blackbrush samples.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Mastication	1	2.066036	91.49	0.00007
Animals/Mastication	6	0.022581	-	--
Location	1	0.323811	21.12	0.00371
Location X Mastication	1	0.069471	4.53	NS
Location X Animals/ Mastication	6	0.015335	-	--

Table 34. Analysis of variance for the in vitro organic-matter digestibility of terminal and basal twigs of masticated and unmasticated blackbrush samples.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Mastication	1	178.3560	11.56	0.01449
Animals/Mastication	6	15.4257	-	--
Location	1	165.7656	129.48	0.00003
Location X Mastication	1	7.5350	5.89	0.05144
Location X Animals/ Mastication	6	1.2802	-	--

Table 35. Analysis of variance for tannin levels in the diets of esophageally fistulated does and kids browsing in heavily and lightly stocked blackbrush pastures from January 2 until March 17 of 1979.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Intensity	1	0.147120	14.85	0.00486
Class	1	0.000062	<1	NS
Intensity X Class	1	0.009539	<1	NS
Animals/Intensity X Class	8	0.009909	-	--
Date	10	0.009402	1.77	0.09343
Date X Intensity	10	0.004611	<1	NS
Date X Class	10	0.004010	<1	NS
Date X Intensity X Class	10	0.005928	1.12	NS
Date X Animals/Intensity X Class	45	0.005299	-	--

Table 36. Analysis of variance for the percent crude protein in the diets of esophageally fistulated does and kids browsing in heavily and lightly stocked blackbrush pastures from January 2 until March 17 of 1979.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Intensity	1	16.842433	21.85	0.00159
Class	1	1.124696	1.46	NS
Intensity X Class	1	0.000608	<1	NS
Animals/Intensity X Class	8	0.770931	-	--
Date	10	1.886482	6.38	0.00001
Date X Intensity	10	1.245701	4.21	0.00037
Date X Class	10	0.709527	2.40	0.02219
Date X Intensity X Class	10	0.517276	1.75	NS
Date X Animals/Intensity X Class	45	0.295686	-	--

Table 37. Analysis of variance for the in vitro dry-matter digestibility of diets consumed by esophageally fistulated does and kids browsing in heavily and lightly stocked blackbrush pastures from January 2 until March 17 of 1979.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Intensity	1	36.837158	2.83	0.13075
Class	1	83.520257	6.43	0.03498
Intensity X Class	1	92.874430	7.15	0.02822
Animals/Intensity X Class	8	12.995903	-	--
Date	10	79.752305	3.12	0.00418
Date X Intensity	10	43.080757	1.69	0.11354
Date X Class	10	18.267908	<1	NS
Date X Intensity X Class	10	18.415559	<1	NS
Date X Animals/Intensity X Class	45	25.535382	-	--

Table 38. Analysis of variance for the percent of time between 8 a.m. and 5 p.m. that esophageally fistulated versus nonfistulated does and kids in lightly and heavily stocked pastures spent browsing from January 2 until March 17 of 1979.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Intensity	1	2,148.54	19.10	0.00048
Class	1	18,189.94	161.72	<0.00000
Fistulation	1	375.65	3.34	NS
Intensity X Class	1	1.50	<1	NS
Intensity X Fistulation	1	96.19	<1	NS
Class X Fistulation	1	1,226.42	10.90	0.00450
Intensity X Class X Fistulation	1	1.11	<1	NS
Animals/Intensity X Class X Fistulation	16	112.48	-	--
Date	10	2,269.38	75.42	<0.00000
Date X Intensity	10	224.17	7.45	<0.00000
Date X Class	10	150.71	5.01	<0.00000
Date X Fistulation	10	38.87	1.29	NS
Date X Intensity X Class	10	71.21	2.37	0.01285
Date X Intensity X Fistulation	10	67.42	2.24	0.01868
Date X Class X Fistulation	10	59.11	1.96	0.04157
Date X Intensity X Class X Fistulation	10	103.37	3.44	0.00047
Date X Animals/Intensity X Class X Fistulation	140	30.09	-	--

Table 39. Analysis of variance for the percent body weight change for esophageally fistulated versus nonfistulated does and kids browsing in heavily and lightly stocked blackbrush pastures from January 2 until March 17 of 1979.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Intensity	1	0.006338	2.02	NS
Class	1	0.009488	3.03	0.10096
Fistulation	1	0.000639	<1	NS
Intensity X Class	1	0.003593	1.15	NS
Intensity X Fistulation	1	0.008597	2.74	NS
Class X Fistulation	1	0.000225	<1	NS
Intensity X Class X Fistulation	1	0.018189	5.81	0.02836
Animals/Intensity X Class X Fistulation	16	0.003132	-	--
Date	3	0.028983	52.79	<0.00000
Date X Intensity	3	0.001216	2.21	0.10217
Date X Class	3	0.002164	3.94	0.01527
Date X Fistulation	3	0.000914	1.66	NS
Date X Intensity X Class	3	0.000242	<1	NS
Date X Intensity X Fistulation	3	0.000151	<1	NS
Date X Class X Fistulation	3	0.000732	1.33	NS
Date X Intensity X Class X Fistulation	3	0.000149	<1	NS
Date X Animals/Intensity X Class X Fistulation	38	0.000549	-	--

Table 40. Analysis of variance for the percent body weight change for does and kids browsing in blackbrush pastures from January 2 until March 17 of 1979.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Replication	1	0.008509	<1	NS
Intensity	2	0.011580	<1	NS
Error A	2	0.016180	-	--
Class	1	0.075614	20.43	0.02025
Class X Intensity	2	0.000922	<1	NS
Error B	3	0.003701	-	--
Date	3	0.136457	52.89	<0.00000
Date X Intensity	6	0.002074	<1	NS
Date X Class	3	0.005509	2.14	0.13135
Date X Intensity X Class	6	0.000770	<1	NS
Error C	18	0.002580	-	--

Table 41. Analysis of variance for the percent body weight change for supplemented and unsupplemented goats browsing in blackbrush pastures from December 29 until March 8 of 1978.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Replication	1	0.008359	<1	NS
Intensity	2	0.028509	2.96	NS
Error A	2	0.009627	-	--
Supplementation	1	0.080767	61.33	0.00434
Supplementation X Intensity	2	0.008954	6.80	NS
Error B	3	0.001317	-	--
Date	4	0.032939	28.74	<0.00000
Date X Intensity	8	0.002540	2.22	NS
Date X Supplementation	4	0.005920	5.17	0.00380
Date X Intensity X Supplementation	8	0.000398	<1	NS
Error C	24	0.001146	1	--

Table 42. Analysis of variance for the percent current season's twig growth in the simulated diets (hand-plucked) of cattle browsing in blackbrush pastures during October of 1979.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Intensity	3	0.226120	24.65	0.00002
Animals/Intensity	12	0.009174	-	--
Date	1	0.239778	26.19	0.00025
Date X Intensity	3	0.049428	5.40	0.01388
Date X Animals/Intensity	12	0.009157	-	--

Table 43. Analysis of variance for tannin levels in the simulated diets (hand-plucked) of cattle browsing in blackbrush pastures during October of 1979.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Intensity	3	0.278156	55.69	<0.00000
Animals/Intensity	12	0.004995	-	--
Date	1	0.404178	47.34	0.00002
Date X Intensity	3	0.078754	9.23	0.00193
Date X Animals/Intensity	12	0.008537	-	--

Table 44. Analysis of variance for the percent crude protein in the simulated diets (hand-plucked) of cattle browsing blackbrush pastures during October of 1979.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Intensity	3	0.908073	5.92	0.01021
Animals/Intensity	12	0.153490	-	--
Date	1	2.847656	22.49	0.00048
Date X Intensity	3	0.321823	2.54	0.10542
Date X Animals/Intensity	12	0.126615	-	--

Table 45. Analysis of variance for the in vitro dry-matter digestibility of the simulated diets (hand-plucked) of cattle browsing in blackbrush pastures during October of 1979.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Intensity	3	131.7374	26.89	0.00001
Animals/Intensity	12	4.8987	-	--
Date	1	379.0322	63.31	<0.00000
Date X Intensity	3	43.2256	7.22	0.00501
Date X Animals/Intensity	12	5.9867	-	--

Table 46. Analysis of variance for the percent of time between 8 a.m. and 7 p.m. that cattle in blackbrush pastures spent browsing during October of 1979.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Intensity	3	188.2387	6.17	0.00886
Animals/Intensity	12	30.5319	-	--
Date	1	313.7512	9.26	0.01023
Date X Intensity	3	25.9738	<1	NS
Date X Animals/Intensity	12	33.8948	-	--

Table 47. Analysis of variance for the percent body weight change for cattle browsing in blackbrush pastures during October of 1979.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Replication	1	0.330625	1.33	NS
Intensity	3	0.550417	2.22	NS
Error A	3	0.247708	-	--
Date	1	38.440000	7.82	0.04896
Date X Intensity	3	2.137917	<1	NS
Error B	4	4.913438	-	--

Table 48. Analysis of variance for the quantity of 36 percent protein block consumed by cattle browsing in blackbrush pastures during October of 1979.

Source	Degrees of Freedom	Mean Square	F	Probability>F
Replication	1	0.004278	<1	NS
Intensity	3	0.187978	3.69	0.15590
Control vs Heavy, Moderate, Light	1	0.556626	10.93	0.04551
Error A	3	0.050911	-	--
Date	3	0.082636	15.51	0.00020
Date X Intensity	9	0.005192	<1	NS
Error B	12	0.005328	-	--

VITA

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Candidate for the Degree of

Doctor of Philosophy

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