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The Trail Boss

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Valuing grazing use on public land

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Abstract

The value of public land forage has been of key interest since grazing fees were first established on federal lands. Additionally, knowing the value of rangeland forage is important for assessing the economics of range improvements, grazing systems, and alternative land uses. It is important for resource value comparisons and impact assessments when public land forage is allocated to other uses. In this synthesis paper, we review the various methods that have been used to value public land forage and discuss the advantages and limitations of each. We highlight that past valuation efforts have concentrated on the value of public land forage for livestock production and, consequently, underestimated total forage value and rancher willingness to pay for forage and grazing permits. These research efforts failed to recognize that amenity and lifestyle attributes from ranch ownership and forage leasing play important roles in the use and pricing of rangeland forage. We review the numerous studies conducted to estimate public land forage value and suggest modifications to improve future value estimates. Because lifestyle attributes of ranch ownership have so strongly influenced ranch values and what ranchers are willing to pay for grazing use on public lands, we find the market value of federal grazing permits and a modification of the standard contingent valuation method for valuing non-market goods to hold the greatest promise for valuing public land grazing.

Key Words: Forage value, grazing fees, grazing leases, hedonic models, contingent valuation, public land grazing

Knowing the value of forage is a necessary component in many economic studies. Forage value estimates are needed for assessing the economics of range improvements, grazing systems, and alternative land uses. Rural appraisers use estimates of forage value in ranch income appraisals. The economic impact of changing forage use and availability starts with an estimate of the economic value of the grazing capacity potentially eliminated or redirected. These assessments and valuations are often controversial, especially when public land grazing is considered.

Much of the prior work to value rangeland forage has dealt with the appropriate grazing fee for public land grazing; the key issue being the level of economic benefits received by grazing users of public lands (Gee 1981, Torell et al. 1993, USDA/USDI

Resumen

El valor del forraje de tierras públicas ha sido de interés clave desde que los pagos por pastoreo fueron establecidos en tierras federales. Adicionalmente, el saber el valor del forraje de los pastizales es importante para tasar la economía de las mejoras al rancho, de los sistemas de pastoreo, y de los usos alternativos del suelo. Es importante para comparaciones del valor de los recursos y evaluaciones de impacto cuando la tierra pública es destinada a otros usos. En esta síntesis revisamos los diferentes métodos que han sido utilizados para valorar el forraje de tierras públicas y se discuten las ventajas y limitaciones de cada uno. Enfatizamos que los esfuerzos de valuación utilizados en el pasado se han concentrado en el valor del forraje de tierras públicas utilizado en la producción de ganado, y consecuentemente han subestimado el valor total del forraje y la disposición del ranchero de pagar por el forraje y por los permisos de pastoreo. Los esfuerzos de esta investigación fallaron en reconocer que los atributos amenidad y estilo de vida de poseer un rancho y arrendar pastizales juegan roles importantes en el uso y precio del forraje. Revisamos los numerosos estudios que condujeron a estimar el valor del forraje en tierras públicas y sugerimos modificaciones para mejorar estimaciones del valor futuro. Dado que los atributos del estilo de vida de poseer un rancho han influenciado fuertemente el valor de los ranchos, así como lo que los rancheros están dispuestos a pagar por el uso de pastizales en tierras públicas, encontramos que el valor de mercado de los permisos federales de pastoreo y una modificación al método estándar de valuación contingente para valorar productos fuera del mercado, como una de las grandes promesas para valorar pastoreo en tierras públicas.

1986). Comparison to private rangeland lease rates has been the primary method to value public forage. Yet, average private lease rates may or may not reflect the total benefit received from the use of range forage on federal lands. Hence, the focus of this paper goes beyond the grazing fee issue and reviews numerous ways forage can be valued on public rangelands. We approach forage valuation from the basis of total value to resource users and consider resource values for livestock production and other values associated with rangelands and ranching that we call quality-of-life (QOL) factors. These amenity and lifestyle attributes from ranch ownership and forage leasing have been shown to play important roles in the use and pricing of rangeland forage. "Forage value" in our application is thus expanded beyond its value for livestock production to include other attributes such as

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exclusive access to permits, the desirable ranching and rural lifestyle, open spaces, and the solitude and tranquil experiences realized or perceived to exist when using public lands for grazing.

In this synthesis paper, we first review the theoretical basis for valuing rangeland forage, both for its value in livestock production and for the value realized from recreation, cultural experiences, open spaces, and scenic views associated with the rural ranching lifestyle. We review the numerous methods that can be used to value forage and discuss the advantages, disadvantages, and limitations of each. We evaluate whether there are regional differences in forage values and relate these differences to the question of whether public land grazing fees should be different for different areas of the West. We recognize there are many values associated with rangelands (USDA 1998). Limiting the scope of this paper to rangeland forage and its use requires a rethinking of the benefits obtained from grazing use of public rangeland.

Over the history of administered grazing on public lands, updates of forage value have varied from periodic appraisals based upon comparable private lands (Rachford 1924, Tittman and Brownell 1984) to indexing values based on private lease rates, livestock prices, and prices paid on a national basis (Dutton 1953, Brokken and McCarl 1987). Updating forage values as markets and grazing conditions change is a critical factor for grazing fee policy. Thus, we discuss different ways public land forage values might be updated through time and how appropriate fee estimates could be established using each of the alternative valuation procedures.

Theoretical Basis for Valuing Public Land Forage

Valuing Forage for Livestock Production

The theoretical justification for various forage valuation procedures has historically been based on the premise that ranchers maximize profit. Forage has a derived demand in the production of livestock, and the forces of supply and demand operate to establish prices within a competitive market (Jensen and Thomas 1967). Establishing the value of public land forage based on its value for livestock production has a long history with strong ties

to the standard production economic model of a profit-maximizing firm. These production principles were first highlighted in an economic model developed as part of grazing fee research conducted in Utah (Roberts 1963). This model formed the traditional basis for valuing forage on public lands.

As shown by Roberts (1963), Nielsen and Wennergren (1970), and Brokken and McCarl (1987), the Utah forage value model implies the standard condition for profit maximization. Profit-maximizing firms use inputs to the point where the value of the marginal product of factor i (VMP_i) is equal to the marginal factor cost of input i (MFC_i). VMP_i is the product of 1) marginal physical product (MPP_i), which is the added productivity (output) of input factor i when used to produce livestock and 2) the marginal revenue from selling the product, which is the price of the product under perfect competition. Under this construct, grazing resources are valued for their MPP and the value of the livestock product to be sold.

By adjusting stocking rates to the level where VMP is equal to MFC , a profit-maximizing level of forage use and output is determined. However, the profit-maximizing level of range forage use might differ from use limits imposed by land management agencies. Roberts (1963) demonstrated that, if the profit-maximizing rancher must set forage harvest where VMP exceeds MFC , an excess value accrues to the permittee. With a long-term lease, this excess value would be capitalized into a permit value, or the value of the base property of the ranch. Thus arises the traditional theory of why public land grazing permits have market value, and the widespread belief that the existence of permit value suggests public land forage is under-priced.

The standard economic model of production and optimal input use implies certain behavioral postulates and requires certain conditions for validity. Observation has shown shortcomings in using the "theory of the firm" to explain the behavior of livestock producers in leasing forage. Most notably, the value of private and public grazing land use does not appear to arise strictly from livestock production (Martin and Jeffries 1966). Ranchers have motives beyond profit that influence their willingness to pay for forage, buy ranches, and remain in business when other investments would provide a higher rate of investment return (Torell and Bailey 2000, Torell et al. 2001).

Valuing Forage for Quality-of-Life Reasons

Buying ranches or leasing forage to obtain the associated lifestyle, as well as the revenue that accrues from agricultural production, suggests a household production framework. Based on work by Becker (1965) and Lancaster (1966a, 1996b), households are said to combine goods and services with time and human capital to produce an output. In this case, ranchers are thought to realize satisfaction and utility from cultural experiences, open spaces, recreation, and scenic views associated with the ranching lifestyle. They maximize utility, of which profit is 1 component, subject to a budget constraint. Ranching as a way-of-life is a good that provides utility and satisfaction to the ranch owner and family.

There are at least 3 indicators that most ranchers are not motivated primarily by profit from livestock production. First, returns to both private and public land ranches are low by any standard measure of investment performance. Depending on ranch size, nominal rates of return from livestock production have typically been reported to range from negative amounts to about 3%, averaging no more than 2% (McGrann 2000, Torell et al. 2001, Smathers et al. 1998b, Workman 1986). By comparison, an American Agricultural Economics Association report on commodity cost and return (CAR) estimation (AAEA 1998) found the nominal opportunity rate that agricultural investors could have made over the 1964–1996 period by investing their money in non-agricultural investments with similar risk was from 5% to 9%.

A second indicator that ranchers do not adhere to a strong profit motive is the relatively small part of land value explained by livestock production value. Trends in ranchland values seem to be impervious to the price of beef and net livestock returns. Adkins and Graeber (1978) found that the productive value of ranches in the Hill Country of Texas accounted for about 10% of ranchland market value, but in the High Plains, the productive value accounted for nearly 50% of market value. Similarly, Pope (1985) found population density, aesthetic differences, quality of deer hunting, and proximity to major metropolitan centers explained most differences in Texas land values. Torell and Bailey (2000) found no statistical relationship between variation in net annual livestock returns or variation in beef prices

and recent trends in New Mexico ranch values. As noted by Barkema and Novack (2000) in an assessment of farm and ranch values in the various Federal Reserve Districts, "During 1999–2000 the value of ranches in the mountain states climbed the most, influenced more by nonfarm investors' demand for scenic mountain views than by ranchers' demand for additional grazing land" (p. 39). It is widely recognized that western ranches are overpriced relative to what the cows will buy and pay for (Torell et al. 2001, Martin and Jeffries 1966).

The third indicator that profit is not the primary motive is that western ranchers list quality of life as a primary reason for ranching. Numerous authors have reviewed the motives of farmers and ranchers (Martin 1966, Martin and Jeffries 1966, Smith and Martin 1972, Harper and Eastman 1980, Biswas et al. 1984, Sullivan and Libbin 1987, Bartlett et al. 1989, Young and Shumway 1991, Gentner 1999, Liffman et al. 2000, Rowe et al. 2001, Torell et al. 2001, Tanaka and Gentner 2001). These studies show, for most agricultural producers, the desirable quality-of-life (QOL) attributes associated with rural living are more important goals than profit maximization.

To help define social and economic characteristics of western public land ranchers, Gentner (1999) conducted a mail survey of Bureau of Land Management (BLM) and U.S. Forest Service (USFS) grazing permittees. The goals and objectives of public land ranchers varied from a high ranking for QOL factors to a strong emphasis on profit maximization for ranchers more dependent on ranching for income. Gentner (1999) found all types of public land ranchers ranked QOL factors above profit maximization as reasons for ranching. This suggests "all ranchers are economic satisficers with varying degrees of importance placed on earning potential from the ranch" (Gentner 1999, p. 49). All ranch groups listed the complementary relationship between land ownership and family tradition, culture, and values as a primary reason for owning the ranch.

Significant policy implications arise when the primary reason for ranch ownership and livestock production is not profit. As noted by Torell et al. (2001), when ranch market values are driven by non-profit factors, disparities will exist between the livestock production value and market value of forage. Traditional economic models used to evaluate land-

use policies will be inadequate and alternative valuation procedures, such as contingent valuation, willingness-to-pay studies, and hedonic models, must be used to consider QOL factors in the forage valuation process.

Methods of Valuing Grazing Use

There are a number of methods that have been used to estimate forage value. These methods have included lease-price observation in the private forage market, comparing total costs (fee and non-fee) of grazing public and private lands, using the value of public land grazing permits to imply the value of forage, economic analysis of factors associated with public land livestock production, competitive bidding processes, and contingent valuation of public land forage. This section summarizes past work on each of these valuation procedures, detailing strengths and weaknesses of each method. Procedures that could be used to update forage values using each method are also discussed.

Market Price Comparison

Leasehold value and comparison to the private forage market is the primary way farms and ranches are valued in income appraisals. Competition for leased forage will supposedly drive lease prices to the value of the marginal product of forage in the production of livestock, and average lease rates indicate earning potential from land ownership. Observed market prices have traditionally been used to calculate expected annual earnings from a ranch property and the capitalized value of the expected future income stream (ASFM-RA/AI 2000).

Comparison to the private forage market is based on the alternative cost doctrine, whereby a profit maximizing lessee of forage will not pay in excess of the amount that must be paid for the next best alternative. Thus, if private and public forage are perfect substitutes, economically motivated ranchers should be willing to pay equal amounts for the 2 sources of forage. Because of policies governing the issuance and regulation of public grazing permits, there is no competition to determine public forage value. Consequently, it has been generally accepted that the fair market value of public lands would have to be estimated indirectly by comparing to the

private forage market (USDI/USDA 1977).

Nearly all valuations of public land forage have used the private forage market to imply value. These comparisons date back to 1916 when the U.S. Forest Service used the rental value of some 900 tracts of private land to determine the apparent market value of Forest Service forage (Dutton 1953). Federal grazing fee studies have continued to rely on private forage market price comparisons as one of the primary indicators of market value (Rachford 1924; USDA/USDI 1986, 1992, USDI/USDA 1977, 1993, 1994).

When tracts of land have comparable characteristics, it is widely believed that comparison to the private forage market is valid. However, adjustments must be made for any observed differences in leasehold arrangements, and it is often difficult to find comparable rental information on ranch properties. Further, the validity of the comparison depends on the assumption of perfect competition. Kearl (1989) questioned this assumption, given the observation that, in many areas of the West, there are relatively few sellers of forage. He felt the forage market was characterized by monopolistic competition with price discrimination, citing the lack of private grazing resources in geographic proximity to public lands as support for his market characterization.

Private landowners often provide rights and services to grazing tenants that are not provided on public lands. These rights and services have value to the lessee that is incorporated into the private land lease rate. Many comparisons to the private forage market have failed to adequately adjust for lessor-provided services and to recognize other lease and land-tract differences. Some of the earliest grazing fee studies did adjust for lease differences. The Rachford (1924) appraisal and lease rate comparison compared 1,675 private land tracts (6.56 million ha) to some 10,000 USFS allotments that had been rated for compatibility based on forage availability, distance to water, topography, and accessibility. When the appraisal results and comparison were presented at public meetings, there was widespread agreement as to the fairness of the comparison method. But, as a business proposition, public land ranchers were unanimous in opposing the fee increases proposed at the time (Dutton 1953). By comparison, the 1986 grazing fee report and mass appraisal of forage (USDA/USDI

1986) was severely criticized by western university economists and others for the minimal adjustments (5% for conditions of use and 10% for lease prepayment) that were made between private and public lands and the mass appraisal procedures used (Dudley and Rostvold 1992, Kearl 1989, USDA/USDI 1992).

Attempts have been made to statistically determine how private land lease rates vary when selected services are provided with forage leases. These studies have generally used regression procedures on a cross-section of private land leases to estimate service and forage values (Gray et al. 1983, Fowler et al. 1985, Torell et al. 1988, Torell and Bledsoe 1990, Rimbey et al. 1992, 1994). Because lessor services tend to be provided in blocks, these regression studies had problems with multicollinearity. Consequently, principal components regression was used to estimate service values in Fowler et al. (1985), and more broadly grouped categories of services were used in the other studies. These studies considered the value of landlord-provided services for daily care of livestock, watering livestock, maintenance of fences and facilities, and grazing access to the leased property. They did not value the hunting, fishing, and timber-harvest rights, exclusion of access to outside parties, and differences in stewardship requirements.

Results of 6 New Mexico lease rate studies, conducted primarily to evaluate the market value of New Mexico State Trust Lands, consistently found the value of landlord services to comprise about 30% of the average lease price (Torell and Fowler 1992). Rimbey et al. (1992) found a slightly higher percentage in Idaho, but this included an adjustment for lease prepayment that was not considered in the New Mexico studies. The Idaho study found the value of services to average 36% or 39% of the average lease price, depending on whether the National Agricultural Statistics Service (NASS) survey lease rate or a University of Idaho survey rate was used.

Using the 30% average service valuation in their calculations, LaFrance and Watts (1995) estimated the average composite real rate of return on private grazing lands was 3.37%. They noted that this value was nearly identical to the 3.35% rate estimated from New Mexico ranch sales by Torell and Doll (1991), and concluded that the 30% average service valuation was appropriate across all 11 western

states. The implied forage valuation procedure was to multiply average private land lease rates reported by USDA-NASS (2001), or other sources, by 70% to estimate net forage value.

Comparison of public forage use to the private forage market have historically assumed the market lease rate reflects the value of forage for livestock production. Yet, the market price comparison method does not necessarily give the value of forage for livestock production alone. Theoretically, ranchers base their willingness to pay for forage on livestock earning potential, but the actual price paid can result for a combination of reasons. Martin and Jeffries (1966, p. 239) noted private and public land forage lessors pay too much relative to livestock earnings potential and concluded, "Evidently private lands are not rented merely for the purpose of profits from beef production either." Recent cost-and-return studies confirm that the willingness to pay more for private leased forage than justified by livestock production has continued (Torell et al. 2000, Smathers et al. 1998a). Leasing private lands provides those who cannot afford to buy ranches the opportunity for livestock income and Quality of Life (QOL) experiences.

Forage values implied from comparison to private grazing markets can be estimated annually. This comparison is currently made each year to update the Public Rangelands Improvement Act (PRIA) fee formula¹. Because lease rate surveys are conducted and published annually, no updating mechanism is necessary.

Perhaps the major limitation of the lease price comparison method is finding private leases that are comparable to public lands and making appropriate adjustments for lease differences that exist. Various lease rate comparison studies support adjusting published NASS private lease rates downward in each state by a factor of about 30% to account for services provided to lessors of private forage that are not provided on public lands, but this percentage is variable and broadly applied. Further, comparison to private land lease rates does not recognize the higher non-fee grazing costs shown to exist on public

lands (USDI/USDA 1977, Bartlett et al. 1993).

Total Cost Approach

The total cost approach is another form of market price comparison that has been used to value public land forage. This valuation approach is based on the belief that "the fair market value of public range forage used for grazing is equal to the lease rate for private forage adjusted by the amount that the cost of grazing on private lands is less than the cost of grazing on public lands" (USDI/USDA 1977, p. 2-19). Comparisons of total fee and non-fee grazing costs on private and public lands are used to estimate the forage value on public lands that would make total grazing costs between the 2 land types equal. The total cost approach explicitly recognizes differences in non-fee grazing costs between private and public lands. Many of the differences in terrain, distance, and facilities are also implicitly considered in the cost comparison.

The total cost approach was used to derive the \$1.23 AUM⁻¹ (Animal Unit Month) base rate used in the PRIA grazing fee formula (USDI/USDA 1977). Total fee and non-fee costs of grazing private and public rangelands were compared using data collected in a 1966 Western Livestock Grazing Survey (Little 1967, 1968; Houseman 1968). The \$1.23 AUM⁻¹ difference in total grazing costs was considered to be the value of public land forage (USDI/USDA 1977). A major point of controversy was excluding interest on the permit investment as a cost item in calculating the base value.

The 1992 Incentive-Based Grazing Fee Study (Bartlett et al. 1993) also used the total cost approach as a forage valuation method. They started with the perception that the total cost approach would give an appropriate valuation of public land forage. The conclusion was that for total grazing costs to be equal on private and public lands, the public land grazing fee would have to be reduced from the 1992 level of \$1.92 AUM⁻¹ to \$0.13 AUM⁻¹. Cost differences were found between USFS and BLM permits and between cattle and sheep producers. The forage value for cattle grazing on BLM lands was \$3.63 AUM⁻¹, but the value for cattle grazing USFS lands was -\$2.86 AUM⁻¹. The estimated forage value for sheep grazing was negative on both BLM and USFS lands. These values suggest, even without a graz-

¹The PRIA fee formula is calculated as $Fee_t = \$1.23 \times (FVI_{t-1} + BCPI_{t-1} - PPI_{t-1})/100$, where FVI is the Forage Value Index, BCPI is the Beef Cattle Price Index, and PPI is the Prices Paid Index. The PRIA formula with modification by Executive Order in 1986 is still used to set public land grazing fees.

ing fee, sheep producers on both BLM and USFS lands, and cattle producers on USFS lands were paying more than those with private leases because of higher non-fee grazing costs.

These results are not consistent with the traditional profit-maximizing model that suggests livestock producers would not pay more to graze public lands than private land alternatives. Further, public land grazing permits will supposedly have grazing value only if total grazing costs on public lands are less than on private land. Yet, the observation is that public land grazing permits do have market value (Torell and Doll 1991, Rowan and Workman 1992, Sunderman and Spahr 1994, Spahr and Sunderman 1995, Torell and Kincaid 1996). Results imply that permit values currently occur without a cost advantage for grazing public lands. This may have changed over time. The traditional economic model explaining permit value apparently held reasonably well in the the 1960s when major grazing fee studies were done to establish the PRIA grazing fee formula. Nielson and Wennergren (1970) found that capitalizing the average difference between total public and private grazing costs from the 1966 Western Livestock Grazing Survey, using an approximate 4% capitalization rate, equaled the average permit value. They concluded that competition and a free market existed for public land grazing permits. Average forage value estimates from their study supported the traditional belief at that time that permit values arise because of a capitalized cost advantage from public land grazing.

Private forage comparison methods fail to meet the profit-maximizing assumption about competitive markets and the derived demand for forage. The complementary value of public and private resources and the personal utility from ranching as a way of life are obvious examples of why ranchers pay more for public forage than livestock earning potential would justify (Bartlett et al. 1993).

Because the total cost approach has yielded inconsistent results through time and because repeating intensive studies to estimate non-fee grazing costs is expensive, additional grazing cost studies are not warranted. Grazing costs could be updated using an index of prices paid, similar to the Prices Paid Index used to update PRIA, but this indexing would not capture differences in the rate of change in grazing costs between private and public lands. Updating forage values could be

done with an index similar to the Forage Value Index (USDA-NASS 2001), but this would ignore the inconsistencies found with the valuation procedure. Estimating livestock grazing cost differences between private and public lands does not recognize the Quality of Life (QOL) reasons for why ranchers are willing to pay as much as they do for both private and public forage.

Permit Value Approach

It is widely believed that the market value of grazing permits arises because grazing fees have been less than forage value. As noted by Roberts (1963), if forage markets are efficient, competition should equalize production costs by inflating ranch values by the capitalized value of any resource underpricing. Past underpricing and the capitalization of permit values have been described as the dilemma we now face in changing grazing fees (Workman 1988, Quigley and Thomas 1989, Torell and Fowler 1992). Past policies have not enabled the federal government to capture all of the benefits of public land grazing.

The underpricing of public land forage when given as the reason for grazing permits having value is largely justified on theoretical grounds, relating closely to the economic models formulated in Utah (Roberts 1963, Nielsen and Wennergren 1970). Empirical evidence, however, on the correlation between permit value and grazing fees is lacking. As noted by USDA/USDI (1992, p. 51), "There is no information on the correlation between the change in permit value and change in grazing fees." This is generally true, but 2 studies (using the same dataset) have found a correlation between ranch values and grazing fees. Torell and Doll (1991) used ranch sales data from New Mexico over the 1979–1988 period to estimate grazing permit values. Hedonic regression models were used to estimate how selected factors affected ranch values, including the apparent cost advantage for grazing on public lands. They estimated that, for every \$1 AUM⁻¹ that public forage is priced below its apparent market value, the value of the ranch increased by \$29.81 AUM⁻¹, which implies a 3.35% ($1 \div 29.81$) capitalization rate.

Using the Torell and Doll (1991) dataset, Xu et al. (1994) demonstrated how to correct a model misspecification by truncating allowable dependent variable estimates (land prices) at zero. With

this adjustment, each \$1 AUM⁻¹ of cost advantage on public lands increased ranch value by \$40.45 AUM⁻¹, implying a 2.47% capitalization rate. In both the Torell and Doll (1991) and Xu et al. (1994) studies, the cost advantage variable was statistically significant at the $\alpha = 0.05$ level. Other authors have relied on the 3.35% capitalization rate to estimate forage value (Torell et al. 1993, Sunderman and Spahr 1994, LaFrance and Watts 1995), but the adjustment suggested by Xu et al. (1994) means a capitalization rate of about 2.5% would be more appropriate. This lower rate of return is similar to the long-term average rate of return western ranchers have made from livestock production (Workman 1986).

The existence of permit value is well documented. Stern (1998) summarized 20 different studies that estimated permit value using various methods. These studies included capitalization of income (Gardner 1962, Lambert 1987); survey and professional opinion of ranchers, appraisers, and real estate brokers (Fowler and Gray 1980, Torell and Fowler 1985); appraisal of ranch sales that were nearly all federal land or where the permit was valued separately (Gardner 1962, Bartlett et al. 1993, USDA/USDI 1992, Salvo and Kerr 2001); and hedonic regression models (Rowan and Workman 1992, Spahr and Sunderman 1995, Torell and Kincaid 1996, Xu et al. 1994).

Permit value estimates range from negative amounts to \$300 AUM⁻¹ (Stern 1998, USDA/USDI 1992, Sunderman and Spahr 1994). Permit values occur without an apparent grazing cost advantage on public lands (Bartlett et al. 1993), and a major part of this value appears to occur for reasons unrelated to livestock production and profit potential. Permit value estimates have been used to assign forage value for a combination of profit from livestock production and utility satisfying behavior (Bartlett et al. 1993). Implying that permit value is solely a capitalized value of excess livestock earning potential, as has traditionally been stated (Martin and Jeffries 1966, Torell and Doll 1991, Bartlett et al. 1993, Sunderman and Spahr 1994), is not appropriate.

The purchase of the grazing permit reflects an amount willingly paid in the competitive ranch real estate market. This value is in addition to the annual grazing fee. It implicitly considers purchaser expectations about future grazing fees, non-fee grazing costs, and land-use poli-

cies, and gives an estimate of value irrespective of the multiple reasons for permit purchase. It captures the rancher's total willingness to pay for public land grazing. A drawback to using permit value to imply forage value is the need to select a subjective discount rate to convert capitalized permit value to annual forage value. Further, estimating hedonic ranch regression models requires detailed data defining ranch characteristics and terms of sale. Past studies in the western states have relied almost exclusively on data provided by Farm Credit Services appraisers. These data are limited or non-existent in some western states.

Estimating forage value using permit value is straightforward after recognizing that both livestock earnings potential and Quality of Life (QOL) values contribute to the value of the permit. Grazing permit value is the capitalized value of annual benefits from holding the lease. Thus, the annual value (A) can be estimated as $A = i \times \text{permit value}$, where i is the discount rate. This annualized value is added to the current grazing fee to estimate the annual value of public land forage (Roberts 1963).

Because grazing permits rarely sell independently of the base ranch, hedonic² ranch value regression models have shown the greatest potential for estimating grazing permit values on a state or regional basis. The level of dependency on public lands varies widely, and federal and state grazing permits are transferable when ranches sell. Thus, an evaluation of ranch sales using hedonic regression models provides a way to estimate permit value regardless of the level of public land dependency. A more detailed description and discussion about hedonic ranch value model use to estimate grazing use values can be found in Bartlett et al. (2002).

Pope (1985) developed an hedonic land value model to evaluate factors that influenced rural land values in Texas. Pope used 1981 data from the Texas State Property Tax Board to estimate per acre expected annual returns for each land parcel studied. Quality of life (QOL) variables considered in the hedonic model included the number of white-tailed deer

harvested per square mile, county population density, acres devoted to agriculture per square mile, highway mileage to various large Texas cities, and dummy variables defining regions of aesthetic appeal. As indicated by R^2 values, Pope (1985) found only 14.7% of the per acre variation in rural Texas land values was explained by variation in annual returns, but the R^2 value increased to 85.8% when QOL variables were included.

Hedonic models used to estimate the value of western ranches have varied from simple specifications to complex equations with numerous variables capturing differences in income-earning potential, location, time of sale, and Quality of Life (QOL) differences. Workman and King (1982) developed a very simple regression model where ranch price (\$ cow unit⁻¹) was related to ranch size (number of cows), distance to markets, time of sale, the value of ranch improvements, and an adjustment for whether the sale included cattle. At the other extreme, Spahr and Sunderman (1995) and Torell and Bailey (2000) included over 20 variables in their hedonic regression models.

In estimating the value of western ranches, hedonic price models have been applied primarily in 2 western states—Wyoming and New Mexico. Sunderman and Spahr (1994) and Spahr and Sunderman (1995, 1998) used Wyoming ranch sales data provided by Farm Credit Services (FCS) to estimate the market value of public land grazing permits and to study property tax inequities caused by the large disparity between livestock productive value and market value of Wyoming ranches. McLeod et al. (1999) used hedonic price models to study the market value of environmental amenities present on Wyoming ranches. Geographical Information System (GIS) data were used to visualize the scenic view at the centroid of a parcel of land and to quantify the abundance and quality of wildlife and fish habitat, as well as accessibility. Alternatively, Spahr and Sunderman (1995, 1998), Sunderman and Spahr (1994), and Rowan and Workman (1992) used a subjective assessment of scenic and recreation potential for each ranch and included this assessment as a dummy variable.

In New Mexico, Torell and various coauthors (Torell and Fowler 1986, Torell and Doll 1991, Xu et al. 1994, Torell and Kincaid 1996, Torell and Bailey 2000) have used hedonic price models to evaluate the determinants of ranch value. These

hedonic models have consistently included percent of grazing capacity coming from public lands, time of sale, ranch size, rangeland productivity, house and building values, and cultivated acreage as explanatory variables. Torell and Bailey (2000) expanded the models to include aesthetic values by defining ranching area dummy variables where aesthetic values were expected to be higher because of mountainous terrain and desirable Quality of Life (QOL) characteristics. Other QOL variables have included distance to town (Pope 1985, Torell and Bailey 2000, Rowan and Workman 1992) and county population density (Pope 1985, Torell and Bailey 2000).

Hedonic models for estimating permit value appear to work well in the southwest where yearlong grazing is practiced. Similar research undertaken on seasonal ranges in Wyoming (Sunderman and Spahr 1994, Spahr and Sunderman 1995, 1998), resulted in inconsistent permit value estimates, with different permit values generated over time and between studies. Northern-state ranch value models do not seem to statistically fit the data as well as the yearlong grazing models appropriate for the southwest. Perhaps QOL values are more important and account for a larger share of ranch value in these northern states. If so, additional detail about the scenic and recreational characteristics and potential of each ranch studied, similar to the efforts of McLeod et al. (1999), will be needed to adequately explain the wide variation observed in ranch value and permit value for seasonally grazed ranches.

Using hedonic models developed for New Mexico, and survey data by Fowler and Gray (1980), the estimated nominal and real value of BLM, USFS, and New Mexico State Trust Land grazing permits in New Mexico from 1966 to 2000 are shown in Figure 1. The average value of deeded land is shown for comparison in those years when hedonic model estimates were available. Since about 1985, the average real market value (inflation adjusted) of USFS and BLM permits in New Mexico have remained relatively constant at about \$100 AUM⁻¹. Multiplying this value estimate by a 2.5 to 3.5% capitalization rate and adding the recent \$1.35 AUM⁻¹ federal grazing fee suggests a nearly constant annual grazing value in the last 15 years of between \$4 and \$5 AUM⁻¹. If 7% is considered to be the opportunity rate of return that ranchers forego by investing in grazing permits

²Economists and real estate analysts describe regressions of the price of a parcel of real estate as related to the characteristics of the real estate using the term "hedonic." Hedonic pricing models are built on the premise that goods traded in the market place have different bundles of attributes and characteristics that influence market value.

Fig. 1. Average nominal and real grazing permit values, and deeded land ranch values in New Mexico, 1966–1999 (From Torell et al. 2001).

(AAEA 1998), and used as the capitalization rate, the implied value of grazing is over \$8 AUM⁻¹. As a regional comparison, recent estimates of average permit value in northern states, where seasonal grazing is common, have generally been between \$35 and \$75 AUM⁻¹ (USDA/USDI 1992, Stern 1998), implying a lower forage value.

If a system is devised to use periodic permit value estimates to imply forage value across broadly defined areas (similar to that used by Bartlett et al. 1993), indexing could be used to provide annual updates until additional studies evaluate changes in permit value. Instead of the Forage Value Index (FVI), an index that tracks changes in asset values (e.g. land and buildings) over time could be developed to provide annual updates. Additional research would be needed to identify a preferred index and the components and weighting of the land value index. As demonstrated by the different trends in permit and deeded land values

shown in Figure 1, an index of private agricultural land values may not be adequate, since public land policy and uncertainty about the future of grazing on public lands are additional factors affecting the value of public land grazing permits. There is no reason to believe the value of grazing permits will necessarily follow the trend of deeded land values, especially if grazing fees are significantly increased and grazing use continues to become more regulated and restrictive.

Production Analysis and Linear Programming

Various production analyses and budgeting techniques can be used to estimate the value of public land forage (Bartlett 1983). These procedures are linked to profit maximization, derived demand, and the value of forage for livestock production.

Using enterprise budgeting, the total gross value of ranch output is calculated and all costs except range forage are

deducted. The remaining value is the residual return to the grazing resource. Dividing the residual return by the amount of forage yields the apparent per unit value of the unpriced forage input (Bartlett 1983).

Linear programming (LP) has been used to estimate forage value (Gee 1983, Kehmeier et al. 1987, Hahn et al. 1989) and to estimate economic impacts from changes in federal land policies (Peryman and Olson 1975, Bartlett et al. 1979, Torell et al. 1981, Gee 1981, Rowe and Bartlett 2001). The dual solution of an LP model provides an estimate of imputed prices for scarce resources, and this shadow price can be used as an indication of marginal value for rangeland forage and other scarce resources. As noted by Brokken and McCarl (1987), a resource shadow price is conceptually similar to Value Marginal Product (VMP) and factor demand. It is different in a strict theoretical sense because the optimal use of other inputs in the production process may change in the LP analysis, but are held constant when constructing VMP curves. The shadow price is affected by product prices, marginal productivity of inputs, and the prices of all inputs.

As an application to forage valuation, Gee (1981) and Hahn et al. (1989) used LP and resource shadow prices to estimate forage value on USFS and BLM lands. Shadow price estimates of forage value in 1981 were estimated to be \$10.86 AUM⁻¹ for BLM and \$11.58 AUM⁻¹ for USFS (Gee 1981). Hahn et al. (1989) updated Gee's work and reported shadow prices for each of 9 USFS regions and a national average. Values ranged from \$9.22 AUM⁻¹ in Region 3 (New Mexico and Arizona) to \$15.11 AUM⁻¹ in Region 5 (California).

Problems have been noted in using shadow prices for resource valuation. Most notably, different shadow prices can be obtained by including different formulations of the constraint set. What costs and where they are included in the objective function also have an impact on shadow price levels. The shadow price estimates of value reported by Gee (1981) measured the return above cash costs per AUM. When depreciation costs and the value of family labor were considered, forage value estimates decreased to \$6.61 AUM⁻¹ and \$7.05 AUM⁻¹ for BLM and USFS, respectively. Hahn et al. (1989) performed additional analyses in which fixed costs and opportunity costs were subtracted from the objective function to estimate long-run shadow prices. These

estimates averaged \$0.49 AUM⁻¹ when family labor, interest on investment, and capital replacement were included as cost items in the LP model.

The difference in short- and long-run shadow prices reported by Hahn et al. (1989) is an example of the differences in shadow prices that can be obtained when the objective function is altered. As noted by Godfrey and Nielsen (1994), it conceptually does not matter whether non-fee grazing costs are included in the Linear Programming (LP) model as a cost to raise a cow or added to the cost of grazing a particular forage resource. Each cow raised will require forage, and non-fee costs can be considered under the "cow-raising" activity or added as a non-fee expense to the "forage-harvesting" activity. The only conceptual problem is to assure that non-fee forage-harvesting costs are counted but not double counted. Godfrey and Nielsen (1994) demonstrated that shadow prices for forage depended on the allocation of non-fee costs between the forage-harvesting and livestock-raising activities.

A wide range of forage values can be justified depending on the parameter definitions of the LP models. Further, given the wide differences in production strategies, resources, and the economic position of western ranches (Gentner 1999), it is likely that numerous models and scenarios would be required to determine forage values from production analysis.

Estimating forage values using production analysis tools, like enterprise budgeting and ranch-level linear programming models, suggests forage value arises only because of livestock production potential. Quality of Life (QOL) values are ignored and the true value of grazing use on public lands will be underestimated. In addition, the expense of building production economic models (generally based upon primary data collection) and breadth of coverage (state or regional) limit their applicability in defining the value of grazing use on public land. Only if the policy or research objective was to determine the value of forage for livestock production would this approach be appropriate.

Competitive Bidding

Establishing a market for public land forage through a competitive bid system has strong theoretical appeal because the forces of supply and demand would define forage value (Gardner 1962, 1963, Martin and Jeffries 1966, Nielsen 1972,

USDI/USDA 1977, USDA/USDI 1992). However, the option of moving to a competitive bid system has been repeatedly rejected by the federal agencies. They believe it would be disruptive to the stability of permittees and rural communities dependent upon public land forage and would not be manageable given the isolated and scattered nature of many public land grazing permits, especially with current permit structure, regulations, and staffing (USDI/USDA 1977, 1993 USDA/USDI 1992).

Competitive bidding for public land forage is done on a very limited basis. For example, forage is leased on a competitive bid basis at the McGregor Bombing Range in southern New Mexico and at Fort Meade in South Dakota (USDA/USDI 1992). Fowler et al. (1994) found that annual bid rates for the McGregor Bombing Range varied greatly depending on rangeland conditions in west Texas and eastern New Mexico. When forage was depleted on area ranches, bidding and bid amounts increased.

If forage is demanded for a combination of profit potential and utility-satisfying behavior, a competitive bid process could be used to determine the market value of public land forage, regardless of the specific motives of the lease participants. Under a competitive bid system, a process would be developed to solicit open, competitive bids for grazing rights on an annual or multi-year basis. If this approach were used, there would be no need to develop an updating mechanism because a market for public land forage would be created and market-clearing prices would be determined through the bidding process. If not all public lands could be competitively leased because of the small or scattered nature of some permits, indexing or average valuation of those that did lease could be used to value those that were not competitively leased or priced.

Contingent Valuation

The contingent valuation method (CVM) has been used to value many different goods, most commonly aesthetic and environmental improvements and recreational activities (Carson et al. 1996, Van Kooten and Bulte 2000). The CVM uses surveys to elicit information about the maximum amount an individual would be willing to pay (WTP) for an amenity or the minimum amount an individual would be willing to accept (WTA) to forgo con-

sumption of an amenity. Theoretically, CVM analysis examines this tradeoff in light of an individual's underlying utility function (u). Following An (2000), a person's WTP for an amenity, offered at a fixed level, is defined as the dollar amount Y that equalizes two indirect utilities such that $V_1(I - Y | Z, \epsilon) = V_0(I | Z, \epsilon)$ where, V_1 and V_0 are the individual's indirect utility with and without the amenity, respectively, I is the individual's disposable income, Z is a vector of observed demographic and other characteristics, and ϵ is a scalar variable representing unobserved personal characteristics. Given the assumption that V_1 is monotonically increasing in u for any fixed (Z, ϵ) , an inverse utility function exists such that $U(V_1(u | Z, \epsilon); Z, \epsilon) = u$ for all $u \geq 0$. WTP can then be expressed as $Y = I - U(V_0(I | Z, \epsilon); Z, \epsilon)$. Using CVM, Y , Z , and I can be elicited from members of a selected population and their WTP assessed by econometric techniques.

While the majority of contingent valuation studies have attempted to value non-market goods, contingent valuation has also been used to value goods traded in markets (Harrison 1989, Kahneman and Knetsch 1992) or quasi-markets (Hof et al. 1989, Carson et al. 1996). Although contingent valuation was originally designed to elicit estimates of use value, recently the emphasis has been on eliciting nonuse values, such as existence values and bequest values (Jakobsson and Dragan 1996).

Contingent valuation is not without its weaknesses in being able to elicit a person's WTP or WTA. The methodology suffers from the same potential biases that are prevalent in survey research, such as interviewer bias and nonresponse bias. But the 2 major concerns with CVM are hypothetical bias and strategic bias. Some researchers contend that a fundamental difference exists between the way an individual makes a hypothetical decision and an actual decision (Neill et al. 1994). Hypothetical bias results from the inability of respondents "to accurately predict how they would behave if a market were created" (Bishop and Heberlein 1990, p. 92). Respondents' understanding of the circumstance or amenity they are asked to value may be limited or imprecise. Individuals may find it difficult to express their value for, or feelings about, an amenity in monetary terms. If respondents rely on a starting bid price presented in the Contingent Value Method (CVM) instrument as an indication of what the value of the amenity should be, starting-point bias

can result (Bishop and Heberlein 1990).

The desire to intentionally mislead the researcher in order to influence policy has been termed strategic bias (Jakobsson and Dragun 1996). Individuals may express an unrealistically high willing to pay (WTP) if they believe they will not actually have to make the payment, yet believe they can influence the desirable supply of the amenity in question by giving a high value. Conversely, they may understate the true value if they feel it will decrease the amount they will have to pay (Bishop and Heberlein 1990).

Contingent Value Method (CVM) is dependent upon primary data gathered through phone or mail surveys, and the data collection expense is high. Given the expense of generating these values, indexing values determined at a point in time appear to be the only possible way of updating values.

In their review of grazing fees and public land management, Rostvold and Dudley (1992) suggested that CVM be used to impute the economic value derived from public land grazing. To date, Hof et al. (1989) has been the only CVM study attempting to elicit WTP for grazing on federal lands. They applied CVM in 4 different formats to value public land forage. Two formats elicited ranchers' willingness to pay, and two examined their willingness to sell. All questions were "open-ended" wherein respondents were asked to fill in a dollar amount representing a maximum willingness to pay or minimum willingness to accept compensation. By comparison, a closed-ended format asks for yes or no responses to a specified dollar amount. Open-ended questions are thought to eliminate starting-point bias. An open-ended format does not offer the respondent information regarding the potential value of the amenity, but allows the individual to devise their maximum willingness to pay or minimum willingness to sell (Bishop and Heberlein 1990).

The price-response formats of the Hof et al. (1989) survey, where respondents were asked their WTP or willing to accept (WTA) in dollar terms, tended to result in either the current federal grazing fee or the private lease rate. This would appear to indicate that respondents were very familiar with the grazing fee issue and might have biased their response on expected outcomes. Quantity-response formats, where respondents were asked to respond to changes in grazing fees in terms of number of cattle they would graze, result-

ed in all or nothing bids; they would respond with either the current number of cattle they grazed or they would respond that they would not graze any cattle.

Using Contingent Value Method (CVM) to value goods, such as public land grazing, may result in biased responses by users who are dependent on the good for their livelihood. Because of this apparent response bias, Hof et al. (1989) concluded that CVM would be an inappropriate way to value public land forage. We feel, however, that CVM may still be a valuable methodology in examining the production and Quality Of Life (QOL) values associated with public land grazing, given recent advances in CVM and a new design of survey methods.

Many of the problems associated with CVM could potentially be rectified by appropriately defining the policy issue to be addressed. Hof et al. (1989) showed that using the grazing fee as the payment vehicle created a strategic bias by respondents. Mitchell and Carson (1987) suggested the payment vehicle must be both realistic and neutral. While the grazing fee is a realistic payment vehicle for federal forage, it is not neutral given the political controversy that surrounds grazing fees. Permit value might be a viable alternative as the payment vehicle. Federal land permittees have argued for decades that permit value is a legitimate cost of grazing on federal lands. Most ranchers purport that permits have value and have been willing to give an estimate of their worth. Asking the question in terms of willingness to pay for a grazing permit, as a one-time payment as opposed to an annual payment, could reduce bias and the direct correlation to the annual grazing fee observed by Hof et al. (1989). One could also ask about Willing To Pay (WTP) for adding to the amount of grazable land or AUMs covered by the permittee's current allotment.

One of the problems associated with using permit value as the payment vehicle in a CVM study is asking the valuation question in a realistic manner. Grazing permits represent a privilege to graze federal forage and are tied to a base ranch property, such as deeded acreage, water rights, and/or livestock. Grazing permits are typically transferred by the agency to another owner when the base property exchanges hands. Therefore, it is important to embed the valuation question in a setting that is both realistic and legal.

Willingness to pay questions are typically used in contingent valuation studies

because of the difficulty in obtaining valid willingness to accept compensation results (Jakobsson and Dragun 1996). Individuals typically have difficulty accepting a compensation scenario when dealing with natural resource issues (Mitchell and Carson 1987). Empirical studies have shown that willingness to accept values are typically 3 to 20 times more than those obtained from willingness to pay questions (Jakobsson and Dragun 1996). Mitchell and Carson (1987) suggested that willingness to accept measures are appropriate if the agent has the right to sell the good in question. With most natural resource assets, the common citizen does not have a vested property right in the good being examined. Conversely, ranchers have been able to transfer grazing permits to others, with the permit being capitalized in the total value of the ranch, implying some level of real or perceived property right. Hence, it might be possible to ask Willing To Accept (WTA) questions in terms of giving up some or all grazable land covered by an existing grazing permit. Testing the experimental design with appropriate focus groups should show if one measure provides better results.

National and Regional Forage Values

One element of the controversy about grazing fees is the belief that forage values throughout the West should be different because of forage type, location, level of range improvement, and a number of other factors. Many believe that, rather than one forage value for all public lands there should be multiple forage values determined by site-specific factors (Robertson 1978, LaFrance and Watts 1995).

For many years, Forest Service grazing fees were based on surveys of comparable private rangeland used to derive forage values on Forest Service rangeland. These values varied by state, national forest, and, in some cases, ranger districts within a forest (Rachford 1924). After 1931, these values were updated by relative changes in livestock markets from base periods of 1921–1930 for cattle allotments and 1920–1932 for sheep (Dutton 1953). Prior to 1968, the USFS had 19 different base grazing fee rates for cattle and 17 for sheep on the western national forests (Nielsen 1972).

In 1969, the USFS and BLM established a nationally uniform grazing fee that was to be implemented over a 10-year period. Prior to completion of the 10-year period, the Public Rangeland Improvement Act (PRIA) was passed by Congress and a new fee schedule established for 1979. The uniform fee policy was based on recommendations from a Western Livestock Grazing Survey (Little 1967, 1968, Houseman 1968) that found total grazing cost (fee and non-fee) differences between ranching areas were not large in relation to differences within ranching areas. The authors concluded that, given the large variability in grazing costs and forage values, one national value for public land forage was justified.

This conclusion was in contrast to Robertson (1978) and others who believed forage values had to vary in different areas of the West and argued for variable fees based on range quality differences. But as noted by Nielsen (1972, p.5), "Many people believe that forage quality should play a vital role in determining grazing fee levels, i.e., the higher the quality and quantity of forage per acre, the higher the fee per AUM. The data available (grazing cost survey data) do not support this notion." Calculating lease rates on a forage quantity basis (\$ AUM⁻¹) eliminated differences observed on a quantity-per-acre basis.

Other researchers have also failed to find significant differences between regions based on cost-of-production studies, largely because of extreme variation in observed grazing costs both within and between regions. Bartlett et al. (1993) and Van Tassell et al. (1997) reported on a comprehensive assessment of grazing costs and forage values estimated across broad ecological regions (Great Plains, Northern Rocky Mountains, Inter-mountain/Columbia Plateau, and others) in Idaho, New Mexico, and Wyoming. These authors found as much variation in grazing costs and forage values within the 12 ecological regions included in the 3 states as between them. They concluded that one national value was justified because statistically valid regions could not be defined.

Several researchers have justified variable grazing fees based upon stratification of ranch sales and/or private lease rates. Spahr and Sunderman (1995) examined Wyoming ranch sales and found that in the Wyoming real estate market grazing permits were valued differently between eco-

logical regions and by type of lease. Similarly, permit values have generally been found to be lower in the seasonal grazing northern states, as compared to Arizona and New Mexico where yearlong grazing is common (Bartlett et al. 1993). Thus, the permit valuation method suggests that annual forage values are lower in the northern states.

LaFrance and Watts (1995) found private lease rate differences among states. They argued that because of these differences, forage values and grazing fees on public lands should also differ by state. They suggested separating the western region into 3 areas for the purposes of calculating forage values on public lands: 1) Arizona, California, and New Mexico; 2) Colorado, Montana, and Wyoming; and 3) Idaho, Nevada, Oregon, Utah, and Washington. Tittman and Brownell (1984) used appraisal techniques to delineate 6 separate pricing areas in the western U.S., based on observed differences in grazing lease rates and other lease provisions. Fowler et al. (1986) used this same data set for New Mexico and suggested 3 separate pricing regions for New Mexico.

Van Tassell and McNeley (1997) also found evidence that private lease rates were statistically different between states in the western region. They used regression techniques to estimate the major factors influencing private lease rates and found these to be lagged yearling price, current year hay price, lagged lease rates, and current input costs. Areas suggested by their analysis included: 1) Washington, Oregon, Idaho, and Utah; 2) Montana, Wyoming, Colorado, Nevada, and California; and 3) Arizona and New Mexico.

Applying the total cost approach to private grazing leases yielded similar variable results. Rimbey et al. (1994) summarized the non-fee costs of grazing on 134 private leases in Idaho, New Mexico, and Wyoming. This study found that New Mexico private grazing costs were statistically greater than those in Idaho and Wyoming.

Perhaps the main conclusion that can be drawn about regional forage values is that they are extremely variable, both within and between states and regions. Houseman (1968) emphasized that cost differences found between allotments should be interpreted as the actual situation and not as an indication of inaccurate data. There is an extreme amount of variation in what people pay to lease forage, and much of this

difference has nothing to do with the value of the forage for livestock production. An obvious implication is that only a competitive market can capture the value of forage on each specific allotment. Further, only those valuation procedures that can capture both livestock production value and Quality of Life (QOL) values can potentially estimate regional differences in the willingness to pay for forage and grazing use on public lands.

Summary and Conclusions

Many forage value studies in the last 40 years have resulted in low or negative estimates of public land forage value. Livestock production returns are low when compared to any standard investment criteria. Yet ranchers still graze livestock on public lands and purchase ranches with grazing permits. We have come to realize that public land forage values include not only traditional livestock production values but also other quality-of-life values, a point that Martin and Jeffries (1966) made over 30 years ago.

Most studies about the value of public land forage have focused on the traditional value of rangeland forage for livestock production. The most common methods used since the original USFS forage value study in 1916 have been the market price comparison and the total cost approach. Production analysis has been used in the last 20 years, particularly to estimate impacts of changes in federal rangeland policies.

Any method of valuing public land forage should incorporate both livestock production value and Quality Of Life (QOL) market influences if the total willingness to pay for public land grazing is to be estimated. This eliminates the use of the total cost and production analysis methods as justifiable public land forage valuation techniques, because they consider only livestock production value. Public land ranchers have demonstrated their willingness to pay more than this value by paying nearly equal total grazing costs (fee and non-fee costs) and additionally purchasing public land grazing permits.

The market price comparison method has traditionally been applied as if forage value arises only from livestock earning potential, but, as noted by Martin and Jeffries (1966), the private forage market also captures other QOL values. To use

private land lease rates as an indication of public forage value requires major adjustments for differences in lease conditions and terms between private and public land leases. The validity of the adjustments will always be questioned and controversial.

Competitive bidding has been proposed as a method to capture the full value of public land grazing (Gardner 1962), but because this method is limited by practical and political concerns about disrupting rural communities and the fairness to current leaseholders, we believe it is not a viable option for all public land parcels. Larger public land parcels could be competitively leased when sufficient competition for the lease exists. Average lease prices for these parcels could then be used to set grazing fees for other parcels that could not be competitively leased because of land-locked location, their scattered nature, or lack of bids.

The permit value approach was originally developed to explain the difference between grazing fees and the apparent market value of public land forage (Roberts 1963). Even as traditional methods, such as the total cost approach used by the 1993 Incentive-Based Grazing Fee study, estimated low values for forage, the permit value approach still resulted in reasonable values. As this was occurring, other research was corroborating Smith and Martin's (1972) declaration that the economic profit motive was only one reason people own ranches and pay what they do for forage.

We believe 2 valuation approaches, Contingent Value Method (CVM) and hedonic regression models, have the most potential for estimating the full market value of public land forage, but these methods require additional refinement, application and testing. While CVM has not been successfully applied to forage valuation studies, it may have the potential to assess the total value or willingness to pay for public land grazing, provided respondents do not associate the valuation with grazing fees and correspondingly provide biased answers. Permit value captures the excess value public land ranchers are willing to pay for public land grazing. It theoretically provides a site-specific estimate of value that incorporates the specific characteristics (e.g., distance, terrain, level of improvement, grazing cost structure, scenic attributes) of each individual allotment. However, permit value is not directly observable in most cases because the value of grazing permits is capitalized

into the total value of the ranch. Hedonic regression models, or the observed value when grazing permits trade without other deeded lands, are required to separate the permit value component.

Significant policy implications arise when the primary reason for ranch ownership and livestock production is not profit. Whittlesey et al. (1993) expounded on some of these implications after noting the same inconsistencies in past forage valuation attempts:

"Extensive cost-of-grazing studies have shown that ranchers, on average, are currently spending as much per unit of forage on public lands (current fees plus costs of use — travel, herding, salting, and so on) as is paid for forage on private lands. Economic theory suggests, therefore, that the value of permits for grazing public lands should be zero, but that is not the case. This leaves some troubling possibilities: our economic models are wrong, ranchers are not profit maximizers, or ranchers benefit from more than forage through the use of the grazing permits. One obvious suggestion does emerge, however. We should cease attempts to discover the 'fair market value' of grazing on public lands for setting the optimal grazing fee and focus our attention on more important and productive issues. Not only is the fair market value of the forage difficult to establish without a bidding process, but it is not the most relevant issue to guide the fee structure for public land grazing." (p. 16).

We agree with nearly all of the points made by Whittlesey et al. (1993). When ranch market values are driven by non-profit factors, disparities will exist between the livestock production value and market value of forage. Traditional profit-maximizing models used to evaluate land-use policies will be wrong (or at least incomplete) for determining the value of grazing use. Ranchers do benefit from more than forage by holding public land grazing permits. The value of forage (or total willingness to pay for forage) will be hard to estimate without an established forage market and the traditional assumption about profit maximization. However, we do not conclude, as Whittlesey et al. (1993) did, that the implication is that we should give up on attempts to estimate forage value. We stick with our earlier con-

clusion that "Additional attempts to define the market value of public land grazing using market price comparisons are not justified" (Bartlett et al. 1993, p. iv), but we believe the economic value of public land forage is an important question to answer. In addition to the obvious application to grazing fees, forage value is needed for evaluating the economics of range improvements, resource value comparisons, and in impact assessments as public land forage is allocated to other uses. There certainly is validity, however, to the major point of Whittlesey et al. (1993) that grazing use of public lands would be more acceptable if the value of grazing exceeded the costs of managing grazing activity and protecting other public values on public rangelands. By using valuation methods that consider all benefits derived from public land grazing, correct benefit/cost assessments of public land grazing can be made.

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Cattle population dynamics in the southern Ethiopian rangelands, 1980–97

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Abstract

Knowledge of livestock population dynamics is important to better understand functional attributes and development potential of pastoral production systems. With a focus on the Borana system of semi-arid Ethiopia for 1980–97, the main objectives of this research were to: (1) Characterize cattle population trends; (2) determine associations of rainfall and stocking rate with change in cattle numbers; and (3) estimate economic losses from cattle mortality. We predicted that the regional cattle population trend would consist of a “boom and bust” cycle with long periods of gradual herd growth punctuated by drought-induced losses. We expected that cattle losses would occur when high stocking rates were combined with large rainfall deficits. Such observations would refute the idea that cattle numbers were erratic and purely controlled by rainfall variation, as predicted by non-equilibrium theory. Cattle dynamics were quantified using herd histories from interviews of 56 households living in 4 sites. Data were aggregated to portray regional cattle population trends and quantify economic losses. Regression analysis was employed to assess associations of rainfall variation and stocking rate with cattle dynamics using 2 approaches: (1) Regional using aggregate herd data, empirical rainfall records, and calculated estimates for stocking rates; and (2) local using site-specific herd data along with recall of rainfall and stocking rate dynamics. Overall, results confirmed that cattle numbers followed a boom and bust cycle. Average cattle holdings dropped from 92 to 58 head/household between 1980 and 1997, respectively. Droughts in 1983–5 and 1991–3 resulted in the deaths of 37 to 42% of all cattle, respectively, up to 15-times higher than net sales. Over 17 years our target population of 7,000 households lost 700,000 cattle with a capital asset loss valued at USD 45 million. Statistical results were more difficult to interpret. Our regional approach indicated neither rainfall nor stocking rate were significantly associated with cattle mortality. We felt this interpretation was erroneous, however, due to a probable—but unmeasured—decline in key

grazing resources that lowered carrying capacity, increased herd instability between successive droughts, and undermined relationships among model parameters. Our local approach was somewhat clearer in that results indicated cattle losses were significantly and consistently associated with rainfall deficits, and occasionally associated with high stocking rates that varied by site. We were concerned, however, about respondent bias and possible error in these results. We concluded that the strongest information we had was simply the aggregate pattern of herd dynamics. When aligned with empirical rainfall records and augmented with data from another dramatic cattle crash in 1998–9, we make the case that stocking rate indeed appears to influence the likelihood that a dry year will reduce cattle numbers. We concluded that the Boran live in a dynamic and productive equilibrium system where land-use change has interacted with rainfall variation to create a vicious cycle of massive cattle losses every 5 to 6 years. Improving human welfare under such circumstances should focus on creating a virtuous cycle based on more timely livestock sales, alternative investment of revenues, and sustainable economic diversification.

Key Words: Borana, pastoralism, drought, equilibrium/non-equilibrium systems, risk management

Resumen

El conocimiento de las dinámicas de la población del ganado es importante para un mejor entendimiento de los atributos funcionales y el desarrollo de sistemas de producción pastoriles potenciales. Enfocados en el sistema Borana de la región semi-árida de Etiopía durante el período de 1980–1997, los principales objetivos de esta investigación fueron: (1) caracterizar las tendencias de la población de ganado bovino, (2) determinar las asociaciones de la precipitación y las cargas animal con el cambio en el número de ganado y (3) estimar las pérdidas económicas debidas a la mortalidad de ganado. Predijimos que la tendencia de la población regional de ganado consistiría en un ciclo de aumento y caídas rápidas con largos períodos de crecimiento gradual del hato puntualizado por pérdidas inducidas por sequía. Esperábamos que las pérdidas de ganado ocurrirían cuando se combinaban altas cargas animal y grandes déficit de lluvia. Tales observaciones refutarían la idea de que los números de cabezas de ganado bovino eran erráticos y puramente controlados por la variación de la precipitación, tal como lo predice la teoría de no-equilibrio. Las dinámicas de ganado bovino se cuantificaron usando los historiales de los hatos de 56 ganaderos entrevistados que viven en 4 sitios. Los datos se agregaron para describir la tendencia regional de la población de ganado y cuantificar Las pérdidas económicas. Se emplearon análisis de regre-

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This paper is dedicated to the memory of Dr. James E. Ellis and his many important contributions to the study of African pastoral ecosystems.

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sión para evaluar las asociaciones de las variaciones de precipitación y la carga animal con las dinámicas del ganado mediante el uso de metodologías: (1) Regional, usando los datos agregados de los hatos, registros empíricos de precipitación y cargas animal calculadas y (2) local, usando los datos específicos del hato por sitio en conjunto con la dinámica de registros de precipitación y carga animal. Los resultados generales confirman que el número de cabezas de ganado bovino siguió un ciclo de aumento y caída rápida. Entre 1980 y 1998 el tamaño de hato promedio cayó de 92 a 58 cabezas/propietario respectivamente. Las sequías de 1983-1985 y 1991-1993 resultaron en muertes del 37 al 42% de todo el ganado respectivamente, hasta 15 veces más que las ventas netas. A lo largo de 17 años nuestra población objetivo de 7,000 propietarios perdió 700,000 cabezas de ganado, con pérdidas estimadas en \$ 45 millones de dólares americanos. Los resultados estadísticos fueron más difíciles de interpretar. El método regional indicó que ni la precipitación ni la carga animal estuvieron asociadas significativamente con la mortalidad del ganado. Sentimos que esta interpretación fue errónea, sin embargo, debido a una probable, pero no cuantificada, disminución en los recursos clave del apacentamiento que bajaron la capacidad de carga animal, incrementaron la inestabilidad del hato entre sequías sucesivas y una relación indeterminada entre los parámetros del modelo. Nuestra metodología local fue algo más clara respecto a que los resultados indicaron que las pérdidas de ganado fueron significativamente y consistentemente asociadas con los déficit de precipitación y ocasionalmente asociados con altas cargas animal que variaron por sitio. Sin embargo, estuvimos preocupados respecto a los sesgos de los entrevistados y el posible error en estos resultados. Concluimos que la información más firme que tuvimos fue simplemente el patrón agregado de la dinámica del hato. Cuando uniformizamos los datos empíricos de precipitación y aumentamos los datos con otra caída dramática de ganado en 1998-1999, concluimos que de hecho la carga animal parece influenciar la probabilidad de que un año seco reducirá el número de ganado. Concluimos que el Boran vive en un sistema en equilibrio dinámico y productivo donde el uso de la tierra ha interactuado con la variación de la precipitación para crear un ciclo vicioso de pérdidas masivas de ganado cada 5 o 6 años. El mejoramiento del bienestar humano bajo tales condiciones debe enfocarse en crear un ciclo virtuoso basado en ventas de ganado más oportunas, inversiones alternativas y la diversificación económica sustentable.

Two models have been forwarded to characterize the ecology of pastoral system dynamics in East Africa. An "equilibrium" model has been proposed whereby herbivores reach population densities at which they exert negative, density-dependent feedback on their own productive performance and degrade or alter natural resources (Lamprey 1983). A "non-equilibrium" model, in contrast, has been proposed whereby climate (i.e., rainfall) variability plays the supreme role in keeping herbivore numbers below a density at which they could negatively affect themselves or influence the environment (Ellis and Swift 1988). The 2 models fundamentally differ in the presumed importance of biotic versus abiotic controls over ecosystem processes. The models consequently vary in the utility of concepts such as ecological carrying capacity, defined as the population density at which there is no net change in secondary production (Caughley 1979). While the concept of ecological carrying capacity is a foundation for managing herbivores and vegetation in equilibrium systems, it can be viewed as irrelevant in non-equilibrium systems (Ellis and Swift 1988, Ellis et al. 1993, Behnke and Scoones 1993).

Coppock (1993) and Dodd (1994) postulated that both equilibrium and non-equilibrium systems occur in Africa, with the former predominating in semi-arid zones and the latter in arid zones. A key factor in whether rainfall variability could control herbivore populations is drought frequency, and drought frequency—along with annual variability in rainfall—tends to increase with aridity (Ellis et al. 1993). A higher frequency of drought reduces the chance that herbivore numbers will steadily grow and increases the chance that the forage base will be dominated by unstable annuals adapted to aridity—a potential problem for the population stability of grazing animals (Coppock 1993).

Coppock (1993, 1994) hypothesized that the Borana pastoral system of semi-arid Ethiopia is primarily shaped by equilibrium dynamics. Observations in the region during the 1980s suggested that cattle production was affected by chronic interactions between stocking rate and annual rainfall, while another consequence of heavy grazing pressure was localized bush encroachment and soil erosion (Coppock 1993, 1994).

The main objectives of this research were to: (1) Characterize cattle population trends for the period 1980–97; (2) deter-

mine associations of rainfall and stocking rate with annual change in cattle numbers; and (3) estimate economic losses from cattle mortality. This approach would allow us to better categorize this production system as equilibrium or non-equilibrium from the herbivore perspective and provide an empirical test of theory. The third objective was part of a risk management assessment. Results were expected to have important implications for pastoral development strategy and policy.

Materials and Methods

Study Area

The Borana Plateau (95,000 km²) is in southern Ethiopia at an elevation of 1,000 to 1,500 m. The northern border of the plateau is about 600 km south of the capital city of Addis Ababa. The plateau extends south to the Kenya border, west to the Rift Valley, and east towards the Ogaden plains.

The regional climate is semi-arid and supports a mixed savanna dominated by perennial grasses (*Cenchrus*, *Pennisetum*, *Chrysopogon* spp.) and woody plants (*Acacia*, *Commiphora* spp.). Annual rainfall in the north-central portion of the plateau—where this work was conducted—typically averages 550 to 700 mm, with 60% received during the long rains from March to May and 30% during the short rains from September to November. A cool dry season occurs from June to August, while a warm dry season occurs from December to February.

The dominant ethnic group is the Boran, who currently number about 325,000 and herd over 1 million head of cattle along with much smaller numbers of sheep, goats, and camels (J. Helland, unpubl.; S. Desta, unpubl.). The Borana production system has been described in detail by Cossins and Upton (1987) and Coppock (1994), but a few points concerning resource use and system dynamics are repeated here. Livestock can range widely in search of forage and water during dry periods, but households in general are increasingly settled for most of the year. Households occur in encampments that are commonly located within 30 km of towns and markets. Cattle are managed as either home-based *warra* herds dominated by milch cows and calves, or more far-ranging *forra* herds dominated by bulls, dry cows, and hardy immatures. Resource use

in the central portion of the plateau is based on a traditional system where about 30 communities (*madda*) are loosely organized with respect to permanent systems of deep wells and associated grazing areas. Human labor required to lift water from deep wells in dry periods has led to an unusually high degree of social cohesion and cooperation in resource use among the Boran compared to many other pastoral societies. Communities located outside of this central portion of the plateau, however, have more heterogeneous forms of social organization and resource use, primarily because dry-season water in these locales is supplied more by ephemeral streams and shallow wells that do not require the same degree of organized labor.

Productivity of forage and livestock is seasonally dynamic, with flushes of primary and secondary production associated with rainy periods. Dry periods, in contrast, are times when green forage and drinking water become scarce, animals lose weight, and people reduce food intake. The traditional diet of the Boran is based on milk from livestock, but this is increasingly supplemented with purchased and home-grown cereals (often maize) as the human population expands and the ratio of cattle to people declines. Grazing lands are becoming more limited as a result of woody encroachment, cultivation, and neighboring ethnic groups crowding the landscape. Food insecurity is an increasing problem (Desta 1999).

Cattle sales are typically low, reflecting a modest need for cash income. Although some animals enter market channels heading north to the Ethiopian highlands, the vast majority of cattle are sold to Kenyan interests that offer higher prices. The cross-border trade has a large black-market component and accurate numbers for these transactions are lacking (Coppock 1994).

Aspects of the development policy environment for pastoralists in Ethiopia are reviewed in Coppock (1994), Desta (1999), and by J. Moris (unpubl.) A few key points will be summarized here.

Pastoral development policy in Ethiopia is not easy to discern—it can change when the national or local government changes, implementation varies by region, and policy is rarely explicit in official documents. It is evident, however, that pastoral people in general have never been a priority for the national government. Indeed, pastoralists tend to be politically marginalized throughout much of the Greater Horn of

Africa when compared to the influences of highlanders and cultivators.

Based on our observations in Ethiopia over the past 15 years, we surmise that the main development goals for the Borana Plateau have included: (1) Promotion of a commercial cattle trade for domestic and formal export markets; (2) maintenance of security; and (3) protection of natural resources, especially endangered wildlife and remnant patches of forest at higher elevations. Large multilateral investments were made in physical infrastructure (roads, livestock market facilities, etc.) and delivery of livestock health services in the southern rangelands during the 1970s and 1980s, and this was intended to set the stage for increased livestock sales by pastoralists. While the physical access to market has increased for the Boran compared to 30 years ago, there is little other evidence that the multilateral investments have directly led to marked improvements in pastoral livelihoods.

Scant resources in the public sector have precluded any broad-based delivery of basic human services (education, health, transportation, etc.) to pastoralists. Literacy rates remain low (<10%) and numerous human health problems remain unchallenged. The Boran therefore still appear to largely fend for themselves and manage their own internal affairs, but under a broad umbrella of government supervision.

Livestock marketing has been a dynamic area for policy intervention. During a period of socialist rule from 1977 to 1991, government interference in livestock and grain markets was pervasive throughout the nation. The Boran were compelled to sell cattle to the state at below-market prices to supply export quotas and provide beef for a large military. Since 1991 the new regime eliminated livestock sales quotas and price controls, and beef prices subsequently increased. Both governments have tried to control illicit cross-border flows of livestock in the hope of recovering more tax revenue, but success has been limited because the borders are difficult to seal off.

Changes in natural resources and land use have occurred on the Borana Plateau in recent years, but these issues have not yet received much attention from policy makers or land-use planners. Local officials and pastoralists express concern about perceived degradation of natural resources in forms such as bush encroachment and soil erosion. Many Boran have

also noted concern with the recent proliferation of locally controlled forage preserves and farming plots that effectively privatize land previously used under rules of common access. These types of problems are thought to ultimately be due to pressure from a growing human population, which in turn has encouraged heavier stocking rates and opportunistic cultivation to meet increased demand for milk and grain production. Importantly, with respect to the main focus of this paper, to our knowledge there has never been a forced, officially sanctioned, de-stocking of pastoral herds on the Borana Plateau in the name of range management, although pastoralists have taken the initiative to implement their own controlled grazing schemes in a few *madda*. Projects to rehabilitate deep wells or create ephemeral ponds have been pursued with caution to reduce the chance for resource degradation associated with water points. A general ban on range fires has been enforced for about 25 years, with an eye towards protecting natural resources from alleged too-frequent burning. This has precluded the traditional use of fire by the Boran for range management and tick control that occurred for centuries. Finally, activities such as charcoal making, unregulated harvest of timber for urban home construction, use of rare trees for rural handicraft production, or harvest of key wildlife species are illegal or otherwise discouraged. Hunting occurs, however, as firearms remain abundant in the system. Possession of firearms by the Boran has been officially sanctioned for many years as one means to encourage a vigilant militia near potentially sensitive international borders.

Predictions and Hypotheses

Although a full assessment of system dynamics should ideally include vegetation as well as herbivores, our focus in this study was confined to the cattle component. This was primarily because our main research objective dealt with risk management, and this required assessment of animal assets at the household level of resolution (Desta 1999). Cattle comprise about 90% of livestock biomass on the central Borana Plateau and thus were the ideal species to investigate because of their dominance. The environment is also relatively favorable in terms of animal health and a general lack of livestock rustling. Net sales of animals out of the system are also quite limited. Cattle herd dynamics,

therefore, are largely determined by the interactions of animals with forage supplies (Coppock 1994).

We wanted to determine the degree to which cattle dynamics have been influenced by stocking rate (equilibrical) and/or rainfall (non-equilibrical) events. Both situations offer distinct predictions.

For a non-equilibrical system, Ellis and Swift (1988) and Ellis et al. (1993) noted that the pattern of livestock dynamics should be density independent, "abiotically driven," and "volatile" in nature. They did not offer an empirical example of livestock dynamics from their study region of arid Turkana District, Kenya, but rather created long-term (65-year) patterns for livestock body condition using a simulation model that portrayed animal nutritional status as a function of forage quantity and quality dynamics (Ellis et al. 1993). Body condition was therefore used as a proxy for other production responses such as lactation, natality, and mortality (M. Coughenour and J. Ellis, pers. comm.). This work suggested that in a non-equilibrium setting, livestock populations should be less able to closely track a highly variable carrying capacity.

For an equilibrical system opposite patterns should hold, namely that population dynamics should be dominated by density-dependent interactions, appear as limit cycles, and exhibit more stability than volatility. This would provide evidence that a livestock population is able to at least intermittently track carrying capacity (Ellis and Swift 1988).

For the semi-arid Borana system, our expectation was that the overall pattern of cattle dynamics over 17 years would reveal a mix of equilibrical and non-equilibrical controls, but tend to be dominated by the former. Specifically, we anticipated that we would confirm a "boom and bust" pattern of herd growth where relatively long periods of herd expansion would be punctuated by sharp, drought-induced crashes. A boom and bust pattern for pastoral livestock dynamics has been observed elsewhere in semi-arid Kenya (Meadows and White 1979, Homewood and Lewis 1987) and wetter areas of semi-arid Zimbabwe (Scoones 1993).

For our research we relied on empirical methods that focused on the determination of cattle mortality as a function of stocking rate and annual rainfall. The selection of cattle mortality as the key response variable is justified in the next section.

If the Borana system is dominated by

non-equilibrical phenomena, an analysis of the effects of rainfall and stocking rate on cattle mortality should reveal that rainfall is most important. In other words, compared to effects of high stocking rates, low rainfall should cause more mortality. Our prediction, however, was that cattle mortality would be affected by both high stocking rate and low rainfall. In particular, we anticipated that the interaction between stocking rate and rainfall would be critical in explaining the dramatic crashes in cattle numbers that have occurred in recent years. We felt that the regional herd would be most vulnerable to drought-induced mortality if stocking rates were high.

We used 2 general analytical approaches in our research. Both approaches relied on cattle mortality data collected from interviews of pastoral households located across 4 study sites, and this is described more fully in the next section. The 2 approaches were somewhat complimentary because they operated at different spatial scales and posed different analytical challenges.

In the first approach we aggregated cattle data across all 56 households to create a pattern of cattle dynamics for the regional herd. We then assessed annual change in regional cattle numbers as a function of regional annual rainfall from official records and regional stocking rates that we estimated using various assumptions. We refer to this as the regional approach. A regional scale of resolution was justified because, particularly during times of drought stress, cattle can move among *madda* in pursuit of forage and water. Social relationships among residents of different *madda* influence reciprocal patterns of resource access (Coppock 1994).

In the second approach we kept the analysis at a local level of resolution (within *madda*) and analyzed cattle mortality across the 4 sites as a function of changes in local rainfall and local stocking rates as recalled by our Borana respondents. We refer to this as the local approach.

Finally, we wanted to make general estimates for the economic consequences of cattle mortality in this system. We expected that cumulative economic losses over many years in a boom and bust cycle could be very high—possibly in tens of millions of USD. Like other traditionally minded pastoralists, the Boran tend to hold cattle for household milk production and as capital assets rather than as a source of

marketable products to generate a steady income stream (Coppock 1994). Hence, the Boran tend to postpone cattle sales during droughts until they have no choice—initial sales usually coincide with a sudden need to buy large amounts of human food (grain), and this happens after the cows have ceased to lactate. This can occur 6 months to even a year after a long drought is underway. This collective behavior that resists capital asset depletion under stress can have disastrous consequences, because by the time cattle are marketed the body condition is poor and the numbers are too large to be readily absorbed by marketing channels. Cattle prices therefore collapse compared to the pre-drought situation, and an accompanying drop in the terms-of-trade of livestock for grain contributes to famine risk (Coppock 1994).

Sampling

The target population for this research was comprised of about 7,000 pastoral households residing within a 35-km radius of the towns of Arero, Mega, Negelle, and Yabello in the north-central region of the plateau. These towns tend to occur at higher elevations having more rainfall than the surrounding areas. Population sizes for the towns ranged from 4,100 (Arero) to 5,240 (Mega), 10,300 (Yabello), and 25,000 (Negelle) based on data in CSA (1996). Distance between towns varies from about 50 km (Yabello to Arero) to 100 km (Mega to Negelle). Urban and peri-urban households typically pursue non-pastoral livelihoods as traders, farmers, etc., and were not considered part of our target population, however. This resulted in "doughnut-shaped" sampling zones with urban and peri-urban populations omitted in the center. The cumulative 15,500-km² area that we sampled represented 16% of the Borana Plateau in terms of size and contained about 15% of the Borana pastoral population (Desta 1999).

The 4 town-based sampling areas are henceforth referred to here as study sites. Study sites varied with respect to rainfall, production systems, and natural resource management (Desta 1999). The Negelle and Arero sites have higher annual rainfall compared to that for Yabello and Mega. The Yabello and Arero sites have more pressure on grazing land from expanding cultivation. The Mega site has the least problems of the 4 sites concerning possible competition between grazing and culti-

vation because the lower rainfall and thinner soils at Mega precludes most farming. The Mega site also has the least potential problems of the 4 with regards to grazing disputes with neighboring ethnic groups, simply because Mega is located in the middle of Borana territory. The Borana traditional form of grazing control based on dry-season access to water in permanent deep-wells (the *madda* system) is most evident in Mega. People in the Yabelo and Arero sites access dry-season water from deep-wells, ephemeral wells, and permanent ponds. People in the Negelle area obtain water more from ephemeral wells and seasonal surface flows. Of all sites, grazing control appears most loosely structured at Negelle. Overall, grazing resources appeared most limiting in relation to population density for the Yabello and Arero sites, hence the expansion of cultivation.

A sampling frame was created by listing all households in the 4 study sites, given there was no official census for us to use. Our list was created using interviews of government officials and pastoral leaders who resided in the scores of villages and encampments that occurred throughout the study sites. The process of creating the sampling frame took 6 months.

Once the sampling frame was completed, key informants were used to help stratify households according to wealth class [i.e., "wealthy," "middle class" or "poor" based on modal ratios of cattle per person of 14:1, 7:1, and 2:1 respectively (Assefa 1990)]. Our sampling design was thus stratified random, blocked by site. Characterization of the target population revealed that 7% of households were wealthy, 37% were middle class, and 56% were poor (Desta 1999). The wealthy owned 28% of the cattle, while the middle class and poor owned 46 and 26%, respectively. We sampled wealth classes in equal numbers and not in proportion with their occurrence, however. We felt that sampling an equal number of households per wealth class would improve the accuracy and comparability of parameter estimates. Calculation of overall means for the target population involved weighting statistics according to the relative abundance of each wealth class.

A sample of 336 households (or 4.8% of the target population) was selected for interview concerning their perceptions of change in the pastoral system, and this work is reported elsewhere (Desta 1999). A sub-sample of 60 randomly selected

households, however, was identified for a detailed analysis of cattle herd dynamics reported in this paper. These households were stratified with 15 per site (5 per wealth class per site). The smaller sub-sample of 60 was selected because the detailed interviews would require more time and effort for each sample unit.

Data Collection and Statistics

Interview Method

Data on cattle population dynamics were collected using interviews that focused on recollections of pastoral households. Such approaches have been shown to be effective with African pastoralists because these people place a very high cultural value on livestock and have well-developed mental skills to track animal inventories (Assefa 1990, Ensminger 1992). A lack of official statistics for cattle populations in this region also required we use this method.

Fifty-six out of the 60 households identified for detailed interviews were successfully located and agreed to participate. The interviews were held with entire extended families covering 2 to 3 generations and took up to 2 days to complete for each household. Respondents were not informed of our predictions to reduce the chance they would tell us what they thought we wanted to hear. Families were asked to form consensus and recall herd histories from 1997 to 1980 in a stepwise fashion. The 17-year period was needed to capture 2 droughts in 1983–5 and 1991–3. The Borana traditional calendar (Legesse 1973) was used along with known benchmark years for droughts and other ecological, social, political, and cultural phenomena to help respondents organize their thoughts. Annual estimates of the household herd size, recruitment, mortality rates, and net sales were obtained. Mortality was also segregated with respect to mature cattle and immature cattle <4 years old, as the latter are more vulnerable to drought, disease, accidents, and predation (Coppock 1994).

Regional Approach for Cattle Dynamics

For the regional approach we wanted to analyze the association of change in current annual rainfall (ΔRF) and previous years' stocking rate (SR) with current annual change in cattle numbers ($\Delta CAT-TLE$) at a regional scale. The logic was that a major increase in current annual

rainfall from the previous year could stimulate herd growth, while a major decrease in current annual rainfall compared to the previous year could lead to more cattle deaths and increased sales leading to a net reduction in herd size. Stocking rate in the previous year would be an indicator of potential resource pressure in the current year. A higher stocking rate in the previous year, for example, could imply that key resources would be rapidly consumed in the current year, especially if forage production was low due to insufficient rainfall. We felt this was the most resolution these data sets could provide. We used a multiple linear-regression model (SAS Institute 1996) that incorporated main effects of ΔRF and SR as well as an interaction term ($\Delta RF \times SR$) on $\Delta CAT-TLE$. Current annual change in cattle numbers was calculated based on total head of cattle averaged across the 56 households for each year. Annual change in rainfall was calculated from empirical data (above) averaged across the 4 study sites in each year. Stocking rates were estimated based on the average number of cattle per household per year (our data) and by invoking a series of assumptions that allowed us to back-calculate numbers of total households and hence estimate total head of cattle from the benchmark of 1997. These assumptions included that: (1) Households had an average of 6.5 people throughout the 17 years, as estimated from data in Assefa (1990), Coppock (1994), and Desta (1999); and (2) human population growth was 2.2% per annum (CSA 1996). This resulted in a time series that began with 4,947 households and 32,154 head of cattle in 1980 and ended at 7,007 households and 45,546 head of cattle in 1997 (D. Coppock, unpubl.). Our ability to make legitimate comparisons of stocking rates over time also required us to assume that: (1) The size of the regional grazing area stayed roughly the same over 17 years; and (2) the ecological attributes of similar stocking rates did not change over time. In other words, under similar levels of rainfall, a stocking rate of 20 head/km² yielded the same degree of resource pressure in the early 1980s as it did in the mid-1990s. This last assumption may have been the weakest of all, as surveys on pastoral perceptions of production system trends indicated that the people felt that the regional carrying capacity was declining (Desta 1999; see Study Area). Despite such perceptions, however, we had no reasonable means to prove that carrying capacity had indeed declined.

Local Approach for Cattle Mortality

For the local approach we wanted to analyze associations of current annual rainfall (RF) and local stocking rate (SR) with cattle mortality (M). In contrast to the regional approach, however, we based this local approach entirely on interview data. In the process of reconstructing herd histories we also asked respondents to recall annual levels for RF and SR on a 5-point, ordinal scale [i.e., very high (5), high (4), average (3), low (2), or very low (1)]. While there was no means to validate recollections for local SR, we could validate recollections for RF using empirical rainfall records. A correlation between empirical data and perceived rainfall levels over 17 years was performed using the non-parametric Spearman's test (SAS Institute 1996).

Reliance on mortality as a primary indicator of herd dynamics has positive and negative aspects. The negative aspect is that mortality is a relatively less sensitive indicator of stocking rate pressure than, say, milk production, weight gain, or even calving rates. The positive aspect, however, is that mortality should be a more objective indicator given our data would be founded on people's recollections. We therefore expected mortality dynamics to provide a reasonable test of predictions. We confined our interview questions to only a few aspects of cattle dynamics—avoiding other details on yearly aspects of cattle production and recruitment, for example—because we did not want respondents to suffer from interview fatigue.

Preliminary inspection of the data indicated that the overall pattern for cattle mortality tended to be episodic. There were extended periods when little or no mortality occurred, but these were punctuated by high-mortality events. We therefore used a 2-stage analysis to determine: (1) The degree to which perceived levels of RF, SR, and the RF x SR interaction were associated with mortality events; and (2) associations of the same factors with the magnitude of mortality once it occurred. It would not be surprising, for example, if a drop in annual rainfall was the factor most strongly associated with triggering mortality events, and a higher stocking rate was the factor most strongly associated with magnitude of death loss once a shock was initiated. The 2-stage analysis also helped us circumvent statistical problems related to meeting normality assumptions for statistical procedures due to a large number of zero-mortality values in the full data set.

The first analysis was based on 176 to 193 observations per cattle age class per site and employed a multiple logistic regression in a doubly repeated-measures design. The repeated-measures variables were household and year and these were both modeled as random effects. The dependent variable was binary, i.e., whether or not cattle mortality occurred for any given household in any given year. A normal-error model is not appropriate for binary response, so a generalized mixed model (Littell et al. 1996) was fit using the GLIMMIX macro in SAS Release 6.12 (SAS Institute 1996) that specified binomial errors and a logit link.

The second analysis also employed a multiple logistic regression in a doubly repeated-measures design. In this case, however, we only used from 41 to 103 observations per cattle age class per site for all instances when mortality differed from zero. Percent mortality was calculated based on household herd size in any given year, and these figures were weighted by the household herd size for more accurate population estimates. Percent mortality was successfully transformed to meet assumptions of normality and homogeneity of variance using the natural log of the angular transformation (Afifi and Clark 1990). A general, linear model was fit using PROC MIXED in SAS Release 6.12 (SAS Institute 1996).

In both analyses data were analyzed separately for each of the 4 study sites because each differed in terms of resource attributes (Desta 1999). Data were also segregated with respect to whether cattle were mature or immature.

Economic Value of Cattle Losses

Our secondary objective, namely estimating the economic value of cattle mortality losses over the 17 years, was performed using mortality data classified by sex, age class, and year. We then multiplied the numbers of animals that died times the respective cattle prices in local currency (Ethiopian Birr). Unpublished records of cattle prices were available from the Southern Rangelands Development Unit (SORDU; a local government agency) and CARE, a non-governmental organization that deals with relief and development. Official rates of currency exchange were USD 1.00 = 2.07 Birr (1980–90) or 5.50 Birr (1991–97). The shift in currency value was associated with a change in government and implementa-

tion of a devaluation policy (Desta 1999). Economic losses per household and per person were estimated on the basis of a target population of 7,007 households and 7.3 people per household for 1997 (Desta 1999).

Results

Rainfall

Considered over 17 years and across the 4 study sites, the mean annual rainfall from the climate monitoring stations was 706 mm with a coefficient of variation (CV) of 25%. This mean was probably biased high compared to the conditions experienced by most of our target population. This is because the monitoring stations are located in the towns, towns are located at higher elevations (as previously mentioned), and rainfall increases with elevation here (Coppock 1994). We considered, however, that the general chronological pattern for rainfall—averaged across the 4 sites—to be a reasonable depiction of the overall situation (Fig. 1).

Regional Cattle Dynamics

General Patterns and Magnitude of Economic Losses

Cattle population dynamics averaged across the 56 households are shown in Figure 2. Two things are apparent, namely a long-term decline in average cattle holdings per household and a pattern of gradual herd growth punctuated by sharp declines. Cattle holdings fell from an average of 92 to 58 head/ household in 1980 and 1997, respectively, a net drop of 37% overall. The sharp declines in inventory were reportedly due to mortality, not sales. Death losses were typically 10 to 15-times higher than net sales (Fig. 2). The net loss of cattle in the mid-1980s was 34 head/household, or 37%. The average household herd then recovered to 85% of the previous peak size by 1990. The subsequent loss of cattle in the early 1990s was 33 head/household or a decline of 42%. The plunges in cattle numbers in the mid-1980s and early 1990s were thus similar in scope and appear to be associated with declines in annual precipitation, although the decline in precipitation observed during the mid-1980s was greater than that during the early 1990s (Figs. 1, 2). Respondents indicated that the vast majority of cattle deaths were due to malnutrition and starvation, with only a

Fig. 1. Annual rainfall for the north-central Borana Plateau, 1980–97, as averaged across 4 meteorological stations at Arero, Mega, Negelle, and Yabello. Data source: Ethiopian National Meteorological Organization (unpubl.).

few due to disease, predation, or other factors (Desta 1999).

Cattle population dynamics for the 3 wealth classes are shown in Figure 3. The average cattle holdings for wealthy, middle-class, and poor households declined from 171, 55, and 40 head in 1980, respectively, to 129, 42, and 16 head by 1997. This represented a net drop of around 25% for the wealthy and middle-class and 60% for the poor.

The average, cumulative loss of cattle due to mortality over 17 years was 327, 107, and 65 head for wealthy, middle-class, and poor households, respectively. This translated into an average economic loss for wealthier households of USD 21,000, followed by USD 6,880 and USD

4,180 for the middle class and poor, respectively. The average loss per household and per person was USD 6,523 and USD 893, respectively. Overall, this can be extrapolated to the target population of 7,007 households, which gives a grand total mortality loss of 710,622 head with a cumulative value of USD 45.7 million.

Associations of Rainfall and Stocking Rate with Change in Cattle Numbers

Results from the multiple regression at the regional scale were paradoxical. They indicated that current annual change in cattle numbers (Δ CATTLE) was not explained by either the current annual change in rainfall (Δ RF; $P = 0.93$), the pre-

vious years' stocking rate (SR; $P = 0.15$), or the Δ RF $\times$ SR interaction ($P = 0.74$).

Data used in this analysis, along with ancillary comments, are shown in Table 1. If we assume the data sets are fundamentally valid and have been properly aligned, it is difficult to discern why neither change in rainfall or stocking rate had significant effects on cattle numbers given the primary sources of mortality given by respondents. One possible explanation, however, is that over time the system was changing in ways that undermined the utility of the statistical analysis. For example, our results could have occurred because of a progressive loss or degradation of drought grazing-reserves (key resources) between 1985 and 1991 (Table 1). Survey respondents have often mentioned that the accessibility and utility of drought grazing-reserves has been compromised by overpopulation, bush encroachment, and renewed tensions along ethnic borders (Coppock 1994, Desta 1999). We therefore speculate that diminished grazing-reserves have contributed to a greater instability of the regional cattle herd in response to drought perturbation, as evidenced by the lagged pattern of cattle losses in 1983–5 compared to the abrupt crash for 1991–3 (Table 1). It is also notable that the cumulative deviation in annual rainfall, as compared to the 15-year mean, was –316 mm in 1983–5, yet only –66 mm in 1991–3 (Table 1). The system thus appears to have been more buffered in response to a greater rainfall shock in the first drought compared to what transpired in the second drought.

If there has been a significant and progressive loss of grazing reserves, it has several unfortunate implications for the validity of the multiple regression. First, it implies that resource pressure from similar stocking rates has grown more intense over time, undermining the analytical utility of our SR variable. Second, a qualitatively different response of the cattle population to each drought markedly reduced the chance for a significant Δ RF $\times$ SR interaction given the relatively short length of time for which data were collected given research objectives (S. Durham, pers. comm.).

Fig. 2. Cattle population dynamics (average number of head/household) aggregated across 56 Borana households for the period 1980–97 and broken-out according to total, total mortality, and net sales. Source: Desta (1999).

Local Cattle Mortality

Perceptions of Rainfall Levels and Stocking Rates

There was a high degree of agreement between the actual occurrence of drought years and the recall of survey respondents.

For example, 87 and 75% of households, respectively, independently identified the drought periods of 1983–5 and 1991–3 as times of low rainfall and hardship. Results from the Spearman's correlation analysis, however, indicated that perceived rainfall levels were not significantly correlated with actual rainfall ($r_s = 0.18$, $P = 0.49$). For stocking rates, survey respondents were fairly consistent within any given study site in their recollection of local stocking-rate levels. Overall, a tally of responses showed that stocking-rate levels were perceived to gradually increase during the inter-drought periods of 1985–90 and 1993–7 (S. Desta, unpubl.).

Associations of Rainfall and Stocking Rate with Cattle Mortality

Results from the statistical analysis of factors associated with the occurrence of cattle mortality over the 17 years are shown in Table 2. These results indicate that mortality events were significantly and often strongly associated with decreased rainfall in each site for both age classes of cattle. Mortality events were significantly associated with increased stocking rates for all cases except mature cattle in the Mega and Negelle sites. Despite the prevalence of main effects for

Fig. 3. Cattle population dynamics aggregated for wealthy, middle class, and poor economic classes of Borana households for the period 1980–97. Economic classes corresponded to variation in ratios of cattle to people. Source: Desta (1999).

rainfall and stocking rate, however, the interaction was never significant.

Results from the statistical analysis of factors associated with the magnitude (percent) of cattle mortality—given mortality occurred—are shown in Table 3. These results indicate that increased magnitude of mortality was consistently and strongly associated with decreased rainfall. Increased stocking rate was associated with increased magnitude of mortality in only 1 of 8 cases, namely immature cat-

tle at Mega. The interaction was significant in 2 of 8 cases, namely mature cattle at Negelle and immature cattle at Arero. The interactions are depicted in Figure 4(a,b). These graphs illustrate that the magnitude of cattle mortality increased as a function of increased stocking rates at lower levels of rainfall.

Table 1. Current annual change in rainfall, previous years' stocking rate, and current annual change in cattle numbers for 56 pastoral households on the central Borana Plateau for 1982–97.

Year ¹	Current Annual Change in Rainfall ²	Previous Years' Stocking Rate ³	Current Annual Change in Cattle ⁴	Comment ⁵
	(mm • yr ⁻¹)	(hd • km ⁻²)	(hd • household ⁻¹)	
1982–3	–50	27	+2	
1983–4	–480	28	–2	First drought year; grazing refugia available
1984–5	–130	28	–22	Second drought year; grazing refugia depleted causing lagged crash
1985–6	+130	22	–5	
1986–7	–10	21	+3	
1987–8	+20	22	+2	
1988–9	+160	23	+4	
1989–90	+90	25	+8	
1990–1	–60	29	+6	
1991–2	–100	32	–18	First drought year; grazing refugia less available than in 1983–4 and they were rapidly depleted, causing current-year crash
1992–3	–80	26	–20	Second drought year; grazing refugia now of little utility, thus crash persists
1993–4	+90	17	+2	
1994–5	–80	19	+6	
1995–6	+20	22	+4	
1996–7	+100	24	+6	

¹See Figure 1 for a depiction of the precipitation pattern in absolute terms. For this analysis 1980–1 was omitted because we were concerned about data outliers, both for rainfall and cattle losses (Desta 1999). The year 1982–3 was therefore the first year we used to calculate current annual change for rainfall or cattle attributes.

²Corresponding annual deviations (mm • yr⁻¹) from the 15-year mean (673 mm • yr⁻¹) were: +377 (1982–3); –93 (1983–4); –223 (1984–5); –93 (1985–6); –103 (1986–7); –83 (1987–8); +77 (1988–9); +167 (1989–90); +107 (1990–1); +7 (1991–2); –73 (1992–3); +17 (1993–4); –63 (1994–5); –43 (1995–6); and +27 (1996–7).

³Calculated based on numbers of households, cattle per household, and growth in the human population. See text for details.

⁴Calculated based on average cattle holdings from interviews of pastoral households.

⁵Official records and expert opinion confirms that multi-year droughts occurred in 1983–5 and 1991–2 (Coppock 1994, Desta 1999). Respondents to various surveys have mentioned that a progressive loss of grazing area has occurred due to population growth in recent decades (Coppock 1994, Desta 1999). Tabulated comments are informed speculation that would help explain varied cattle dynamics for the drought periods of 1983–5 and 1991–3.

Fig. 4(a,b). Interaction between stocking rate and rainfall for magnitude of mortality for (a) immature cattle at the Arero site and (b) mature cattle at the Negelle site for the period 1980–97. Rainfall and stocking rates were based on recall of respondents from group interviews and were scaled as: 1 (very low), 2 (low), 3 (average), 4 (high), and 5 (very high). Immature cattle were those <4 years old while matures were all other cattle. The Negelle site had only 3 stocking rates compared to 5 for Arero. Source: Desta (1999).

Discussion and Conclusions

Overall, our research has provided useful information and a valid test of theory given the complexity of the pastoral system, the lack of ancillary or validation data, and limitations of our survey methods. The core data set for cattle dynamics is reasonably accurate despite being based on recall. Consistency among respondents in establishing a calendar of events, their intimate knowledge of cattle inventories, and the relatively few sources of change for cattle numbers reduced the scope for accounting errors.

Some of our statistical analyses yielded puzzling results, but we believe these can be reconciled. We better recognize why complex system dynamics can be poorly suited for conventional statistical analysis. Scoones (1993) also noted the difficulties when attempting to precisely identify regulatory factors affecting “real-world” populations. In the following discussion, therefore, we concentrate more on the simplest descriptive evidence to build a case that equilibrational controls—embodied by periodic interactions between rainfall and stocking rate—predominate in this semi-arid system.

Regional Cattle Dynamics

Results from our statistical analysis at the regional scale were indeed paradoxical—they indicated that neither annual change in rainfall or the previous years’ stocking rate significantly affected current annual change in cattle numbers. While we believe the data sets used in the regional analysis are valid, we strongly assert that the statistical implications are easily misinterpreted. The problem likely occurred because we omitted an essential third factor from the analysis—a loss of grazing refugia between 1984 and 1991—that reduced carrying capacity and increased herd instability in response to rainfall deficits. This altered the quantitative relationships among rainfall deficits, stocking rates, and cattle mortality to an extent that successive drought events were not statistical replicates, even though the overall magnitude of cattle mortality was similar for each case. We thus focus the remainder of this discussion on the basic pattern of regional herd dynamics along with annual rainfall data because they alone are very revealing.

The strongest evidence that cattle numbers on the Borana Plateau are primarily governed by stocking-rate factors is the overall boom-and-bust pattern for regional herd dynamics. We interpret the gradual growth of the regional herd over 6 years from 1985 to 1990, and over 4 years from 1993 to 1997, as evidence that the population attempts to track a carrying capacity. Cattle numbers indeed collapse in response to a rainfall deficit, but the system is primed for catastrophe by population size. If cattle dynamics were non-equilibrium and thus rainfall-driven, we should have observed a far more erratic or volatile pattern (Ellis and Swift 1988, Ellis et al 1993).

Our time-series data are now augmented by other observations from the late 1990s that add credence to the idea that herd crashes are becoming a more regular—and hence a more predictable—feature of this production system. Shibru (unpubl., 2001) reported another population crash on the central Borana Plateau during 1998–9 that claimed 62% of the cattle population. His findings were based on 2 distinct surveys of 89 and 137 pastoral households. The rainfall for 1998–9 was 318 mm (Shibru, unpubl.), or about half of a 17-year mean of 637 mm (Desta 1999). The crash of 1998–9 was the culmination of another 5 years of herd growth that started in 1993.

Table 2. Associations of annual rainfall (RF), stocking rate (SR), and interaction between rainfall and stocking rate (RF x SR) with occurrence of cattle mortality (i.e. probability of mortality Pr(M)) during 1980–97 from values reported by 56 Borana households across 4 study sites in southern Ethiopia¹.

Study site	Age Class of Cattle ²					
	Mature			Immature		
	RF	SR	RF x SR	RF	SR	RF x SR
Yabello	**	**	NS	**	**	NS
Mega	***	NS	NS	***	*	NS
Arero	**	**	NS	***	*	NS
Negelle	*	NS	NS	***	*	NS

*, **, ***Significant at 0.05, 0.01, and 0.001 levels, respectively.

¹Based on multiple logistic regression of mortality occurrence in a doubly repeated measures design (Desta 1999). For example, the regression equation for Yabello mature cattle is:

$$\text{Pr}(M) = \exp(g(\underline{x})) / (1 + \exp(g(\underline{x}))), \text{ where } g(\underline{x}) = 0.893 - (0.716 \cdot \text{RF}) + (0.264 \cdot \text{SR}) - (0.093 \cdot \text{RF} \times \text{SR}).$$

²Immatures were <4 years old and matures were all other cattle. The degrees of freedom were as follow: Yabello matures (175), Mega matures (173), Arero matures (181), Negelle matures (190), Yabello immatures (175), Mega immatures (173), Arero immatures (181), and Negelle immatures (190).

Based on our data and that of Shibru (unpubl., 2001), we postulate that the interval of 5 to 6 years between crashes is primarily determined by the time required for the regional cattle herd to grow and reach a density at which grazing resources become heavily utilized—this is when the regional herd becomes vulnerable to sudden deficits in forage supply. The rapid growth potential for cattle numbers is encouraged by the relatively favorable production environment (see Study Area). Although a declining carrying capacity has been postulated, and this makes estimation of critical thresholds problematic, we would speculate that vulnerability of the regional herd to forage deficits markedly increases when cattle numbers exceed on the order of 20 head/km², or 310,000 head for our study region. Once the population has exceeded a critical density, sudden feed shortages—and high rates of cattle

mortality—can occur in response to even a minor dip in annual rainfall. If the hypothesized loss or degradation of key grazing refugia continues to occur, we would expect the interval between herd crashes to decrease.

While the herd crashes of 1983–5, 1991–3, and 1998–9 were initially triggered by years that were drier than the preceding year, not all of the “trigger years” were equally “dry” when compared to long-term averages. We therefore hypothesize that the occurrence and magnitude of each crash is differentially affected by rainfall deficit and stocking rate. This is why conventional statistics can be problematic for such an analysis. For example, our empirical information suggests that the crash of 1991–3 was more strongly related to high stocking rates than a rainfall deficit, while the crashes of 1983–5 and 1998–9 appear

more strongly related to both rainfall deficits and high stocking rates. We posit that the magnitude of each crash is defined by the size of the rainfall deficit in relation to the stocking rate in the “trigger year.” We hypothesize that the higher the stocking rate and lower the rainfall, the larger the crash.

Perhaps an even more direct illustration of the important role of stocking rate in cattle crashes is the observation that not every “dry” year in the 17 covered by our research produced a crash. For example, the years 1986–8, 1992, and 1994 had rainfall on the order of 580–600 mm per annum—typically as “dry” or “drier” than most years that produced crashes—but cattle mortality was very low at these times. We surmise that the reason mortality was low in these years was because stocking rates were low. Stocking rates were low because herds were at reduced numbers during periods of herd recovery following previous crashes.

Recent reconnaissance on the Borana Plateau provides more information that helps complete a picture for cattle dynamics at the regional scale (S. Desta, pers. obs.). The long rains appear to be considerably above average by mid-2001, with one result being some of the largest standing crops of forage in recent memory. The regional cattle herd still appears small in number, however, as it is still recovering from the crash of 1998–9. Given this scenario, we expect the next regional cattle crash will be most likely to occur by 2005. The pastoral population thus finds itself in a “vicious cycle.”

Local Cattle Mortality

Perceptions of Rainfall and Stocking Rate

The statistical results for the associations of stocking rate and rainfall with cattle mortality at the local scale produced some results that were equivocal compared to our interpretation of factors affecting cattle dynamics at a regional scale. The statistical results suggest that main effects of stocking rate, and interactions between stocking rate and rainfall, were relatively minor compared to the main effect of rainfall. This was especially the case for the magnitude of cattle mortality, which is the main response variable of interest when examining possible density-dependent interactions.

We must be particularly cautious, however, about making detailed interpretations

Table 3. Associations of annual rainfall (RF), stocking rate (SR), and interaction between rainfall and stocking rate (RF x SR) with percent cattle mortality during 1980–97 from values reported by 56 Borana households across 4 study sites in southern Ethiopia. These analyses examined the magnitude of mortality given that mortality occurred; zero mortality values were omitted¹.

Study site	Age Class of Cattle ²					
	Mature			Immature		
	RF	SR	RF x SR	RF	SR	RF x SR
Yabello	***	NS	NS	***	NS	NS
Mega	***	NS	NS	**	***	NS
Arero	**	NS	NS	***	NS	*
Negelle	***	NS	**	***	NS	NS

*, **, ***Significant at 0.05, 0.01, and 0.001 levels, respectively.

¹Based on weighted multiple linear regression of the transformed (log-arc-sine-square root) percent mortality in a doubly repeated measures design (Desta 1999), with total herd sizes as weights. For example, the regression equation for Yabello immature cattle is:

$$\text{Percent mortality} = 100\% \times (\sin(h(\underline{x})))^2, \text{ where } h(\underline{x}) = -0.576 - (0.251 \cdot \text{RF}) - (0.0306 \cdot \text{SR}) + (0.0106 \cdot \text{RF} \times \text{SR}).$$

²Immatures were <4 years old and matures were all other cattle. The degrees of freedom were as follow: Yabello matures (100), Mega matures (47), Arero matures (82), Yabello immatures (87), Mega immatures (38), Arero immatures (44), and Negelle immatures (54).

of these results. This is primarily because we are concerned that selective memories of respondents could introduce differential degrees of accuracy, especially with respect to the scaling of rainfall or stocking rate. Our correlation analysis indicated little agreement between perceived versus actual rainfall, but we concede that local rainfall may have substantially varied from that measured at climate stations located at higher elevations, often many kilometers away. The people were able to reliably identify years of drought and crisis, and deserve credit for that. Our concern, however, is more related to our speculation that drought years could be remembered in more vivid terms than years of higher stocking rates. Although we offer no proof, we suspect that stocking rate could be harder to accurately scale from memory compared to rainfall. This problem could be compounded by pastoral management practices that attempt to mitigate high stocking rates through herd dispersal during periods of crisis. For example, during droughts cattle can be rapidly moved from local *warra* sites to distant *forra* locations to reduce stocking rates near homesteads and help conserve local forage and water resources (Coppock 1994, Desta 1999). Such herding practices could make it more difficult for respondents to accurately gauge stocking rates during stress years.

If we assume, however, that these results have a reasonable degree of accuracy, and accept the idea that the association of cattle mortality with rainfall deficits is probably biased to some degree by more vivid recollections of respondents compared to those concerning stocking rate, several issues merit exploratory comment. First is site variability. Although all aspects of cattle mortality were strongly associated with decreasing rainfall regardless of site, site variation did occur with respect to influences on mortality associated with an increasing stocking rate, either in isolation from, or with respect to, interactions with rainfall. This site variation makes sense in light of potential differences in resource endowments and the degree to which each site is bounded or flanked by potentially competitive neighbors (see Study Area and Sampling). Based on such criteria, we could expect, for example, that cattle in the Negelle site could exhibit the lowest degree of density-dependent interactions compared to those in Arero, Mega, and Yabello. No such pattern emerged, however, either for occur-

rence or magnitude of mortality. Thus we lack an explanation as to how influences of stocking rate could vary by site. The second issue concerns potential variation in factors affecting mortality for mature versus immature cattle. We could expect, for example, that compared to mature cattle, mortality of immatures would be more influenced by stocking rate. This is because immatures are often kept close to homesteads in "sacrifice zones" during stress periods and thus potentially subjected to acute resource restrictions (Coppock 1994). The observed pattern for occurrence of mortality gives some support to this contention, but this is not the case for magnitude of mortality. Both issues of mortality variation due to site and age class of cattle thus remain muddled. A comprehensive, site-specific study of resource and management dynamics would be required to clarify hypotheses.

Synthesis of Cattle Dynamics

The most cautious, and thus most appropriate, conclusion from our work is that both equilibrial (stocking rate) and non-equilibrial (rainfall) factors influence cattle dynamics on the Borana Plateau. Our conclusion echoes to some extent work by Scoones (1993). He found that cattle populations over a 63-year period in communal areas of semi-arid Zimbabwe tended to be regulated by density-dependent factors acting on birth and death rates during "normal" years, but that numbers were also periodically limited by density-independent factors such as drought.

It is obvious, as in other pastoral systems, that livestock numbers and animal productivity vary from year to year on the Borana Plateau. While some may interpret any deviation from static conditions as evidence of non-equilibrium dynamics (Sidahmed 1993), the defining process for an equilibrial system is density-induced, negative feedback (Berryman 1989). Equilibrium conditions therefore exist as long as a population oscillates around some mean, regardless of the amplitude. Hence, a highly variable system can still be an equilibrial system. Indeed, making allowance for a likely downward trend in carrying capacity and inevitable noise in the data, the boom-and-bust pattern for cattle numbers in southern Ethiopia almost resembles a limit cycle, indicative of a prevailing influence of stocking-rate over herd dynamics. Although rainfall deficits can indeed trigger calamitous cattle losses

here, we contend that effects of rainfall deficits are magnified or mitigated by stocking level.

Despite having put our foot more firmly in the equilibrial camp for southern Ethiopia, we have little problem believing that hot, very arid systems such as that in South Turkana, Kenya, can have livestock dynamics largely driven by climate variability (Ellis and Swift 1988). Turkana cattle, in particular, depend on a highly unstable herbaceous layer dominated by annual grasses and forbs. When the long rains fail in South Turkana, there can be no herbaceous cover on the sandy plains or lava hills, regardless of animal numbers. Then animals must trek to grazing refugia in steep montane regions or nomad's lands between ethnic territories, often at great peril to herders and stock (Coppock et al. 1986a).

We also realize that the reliance on livestock numbers as our main response variable was a conservative choice. Had we been able to focus on milk production, for example, a higher degree of climate effect could have been observed given the role that rainfall events play in greening-up forage, improving livestock nutrition, and spurring lactation (Coppock et al. 1986a, 1986b). Mortality in particular was logical for us, however, given our reliance on recall information and a focus on household capital assets.

Our research at least indirectly points to the importance of key resources in understanding pastoral system dynamics. Illius and O'Connor (1999) contended that animal numbers in African pastoral systems are regulated in a density-dependent fashion by limited forage in key resource areas. They noted that strong equilibrial forces thus occur over a limited part of pastoral systems, and effects elsewhere are more heterogeneous. Our experience offers some support for this concept. More study of key resources is required, however, to clearly confirm that loss of grazing refugia is contributing to system instability in southern Ethiopia.

Our results also suggest that when characterizing patterns of cattle dynamics, and hence making interpretations about equilibrial or non-equilibrial influences on population processes, scale of resolution matters. For example, at a local scale we have ample evidence that households can vary in the degree that their herds are affected by calamity—some may be wiped out while others suffer relatively little (Desta 1999). Such differences could be

related to pure luck and/or variability in management skills, access to social reciprocity networks, resource dynamics, local precipitation, etc. Potentially erratic or volatile patterns of local herd dynamics could appear to be driven by density-independent factors. At a regional scale, however, we would speculate that a smoothing effect emerges as a result of aggregating many local outcomes. This aggregated pattern serves to dampen volatility and therefore appears to reflect more density-dependent influences. The simplest explanation for effects of scale would be a “zero-sum” nature of cumulative grazing interactions. For example, animals that die at one locale can create a potential pocket of surplus resources accessible to animals from elsewhere. Such reciprocity in resource use is inherent in the traditional *madda* system (see Study Area).

Comments on Vegetation Change

Vegetation analysis per se was not part of this particular research project, but some comments are warranted—in the context of non-equilibrium concepts—with regards to previous work on vegetation change that has been conducted on the Borana Plateau. Both plants and animals should be considered in a comprehensive examination of theory.

In a climate-driven system, vegetation dynamics should be primarily driven by factors such as moisture variability rather than herbivory (Ellis and Swift 1988). It has been found that vegetation in arid environments tends to exhibit more non-equilibrium features, while vegetation in mesic environments is more subject to equilibrium influences (see review in Illius and O'Connor 1999, Fernandez-Gimenez and Allan-Diaz 1999).

The issue of what controls vegetation change is particularly important for pastoral systems in developing countries because erroneous assumptions can lead to inappropriate policy and hence, even more problems for people. For example, in a non-equilibrium setting, pastoralists could inordinately suffer in economic terms from forced de-stocking to reduce damage from overgrazing, when in fact climate is driving negative trend in resource condition (Ellis and Swift 1988, Scoones 1993). The converse, however, is also a problem; namely, assuming that a negative trend in resource condition is attributable to climate and thus absolving land users of their responsibilities for stewardship (Illius and O'Connor 1999).

The best available empirical information for the Borana Plateau indicates that bush encroachment and erosion of surface soils has widely occurred over the past few decades, particularly at higher elevations in upper semi-arid and sub-humid locations (Billé 1985, Coppock 1993, 1994). Proliferation of woody plants has occurred at both local and regional scales; this distinction is important because regional-scale change can be more attributable to climate effects, while local-scale change can be more attributable to management or utilization practices (Mortimore 1989; Stafford-Smith and Pickup 1993; Fairhead and Leach 1996). Bush encroachment on the Borana Plateau is proposed to occur in response to heavy grazing and lack of fire. Lack of fire is related to a grazing-related reduction in herbaceous fuel and policy that has banned burning since the mid-1970s (see Study Area). The heavy grazing pressure is thought to have arisen as a result of increased sedentarization of pastoralists and their herds. This has resulted from several factors including development of permanent ponds, a steady increase in human and livestock populations, and the increasing allure of towns and markets. We therefore believe that livestock (cattle) are also a source of substantial vegetation change in many parts of the Borana Plateau. This reinforces our contention that we are dealing with a dynamic and multi-faceted equilibrium system.

Development Implications

We contend that pro-active management has a much greater role to play in dynamic equilibrium systems compared to that for non-equilibrium systems. If herd crashes—and hence massive losses of capital assets—are mediated by stocking rate, then stocking rate could serve as a fairly reliable early warning tool to promote hedging behavior for pastoral risk management. One idea, given an increasing likelihood that households will regularly suffer from herd depletion, is to promote more-timely sales of less-productive animals before crises occur, and direct these revenues into sustainable development schemes that encourage forms of economic diversification that complement traditional livelihoods. We remain firm in our prediction that another cattle crash is most likely to occur on the Borana Plateau by 2005. This gives pastoralists and development agents a timeline to implement risk-management interventions that could better buffer the local population.

There is an important distinction between advocating some timely de-stocking to promote a measure of herd stability and economic development, versus the time-worn (and usually failed) approach of official coercion to de-stock in the name of environmental protection—the latter has been often attempted elsewhere in Africa. We suspect the former approach would be far more fruitful with people like the Boran who are increasingly living on the margins of social and economic security. They are looking for new options to augment their livelihoods (Desta 1999).

Cattle mortality represents a significant economic loss to Borana society. The average annual loss of USD 384 per household is nearly 3-times the average annual cash income of USD 135 (Coppock 1994). To illustrate further, if our results are extrapolated to the entire Borana Plateau where drought impacts have been similar, the loss of livestock wealth could exceed USD 300 million since 1980. If pastoral systems from northern Kenya are included over the same time frame, combined losses for cattle alone could exceed USD 750 million, while adding losses of small ruminants and camels could make grand total losses over USD 1 billion (P. Little, pers. comm.). Capturing even a fraction of such losses could be a useful start. The approach could include creating a virtuous cycle involving improved marketing, enhanced rural finance, viable alternative investments, and ultimately economic diversification (Desta et al. 1999).

Efforts to regain some measure of system stability in response to drought could also involve rehabilitation and management of key resources and thus restoration of traditional mobility patterns. This would help communities to again be able to respond to crisis in adaptive, traditional ways. Community investment that prioritizes relocation of people who now reside in former (unoccupied) grazing refugia could be an important first step in this process.

Finally, we urge that more researchers broaden their attention from detailed analyses of plant and animal population dynamics to include human population dynamics in pastoral systems. This and other work conducted in southern Ethiopia points to human population growth as a critical variable that explains much of the change in resource use and one that can illuminate new windows of opportunity for development intervention.

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Effects of water quality on cattle performance

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Abstract

Water is an important nutrient for livestock production and is often provided on rangelands directly from ponds or dugouts. Cattle may defecate and urinate into the water thereby adding nutrients and reducing palatability. A study was conducted to examine the effects of water source on cattle production and behavior, to determine the relationship of selected chemical and biological constituents on the observed response and to test the effect of fecal contamination on water consumption. Four dugouts or ponds were selected at 4 sites: 2 in the Fescue Prairie near Stavely in southwestern Alberta, 1 in the Mixed Prairie at Onefour in southeastern Alberta, and 1 in the Palouse Prairie near Kamloops, British Columbia. Yearling Herefords were tested at 3 sites and Hereford cow-calf pairs at 1 Stavely site. At each site, three paddocks radiated from the pond that were stocked with 10 yearlings or cow-calf pairs randomly assigned to either clean water (water delivered to a trough from a well, river, or pond), pond water pumped to a trough (pond_{trough}), or direct access into the pond (pond_{direct}). The trials were repeated at each site for 3 to 6 years. Observations were made on cattle weight gains, cow backfat thickness, and activity budgets. Fecal samples were analyzed for selected parasites and pathogens. Other experiments were conducted to determine the effects of manure-contaminated water on feed and water consumption and water selection. Calves, with cows drinking clean water, gained 9% more ($P < 0.10$) weight than those with cows on pond_{direct} but cow weight and backfat thickness were not affected. Yearling heifers having access to clean water gained 23% ($P = 0.045$) and 20% ($P = 0.076$) more weight than those on pond_{direct} and pond_{trough}, respectively. Cattle avoided water that was contaminated with 0.005% fresh manure by weight when given a choice of clean water. Cattle that had access to clean water spent more time grazing and less time resting than those that were offered pond_{trough} or pond_{direct}. Cattle management must consider water quality together with forage conditions in order to achieve optimal production from rangeland.

Resumen

El agua es un nutriente importante para la producción ganadera y se provee a menudo directamente en los agostaderos de las charcas o de los aguajes. El ganado puede defecar y orinar en el agua y de ese modo agregar nutrientes y reducir la palatabilidad. Un estudio fue conducido utilizando ganado vacuno de la raza Hereford para examinar los efectos de la fuente de agua en la producción y el comportamiento del ganado, para determinar la relación de componentes químicos y biológicos seleccionados en la respuesta observada y para probar el efecto de la contaminación fecal en la consumición del agua. Cuatro aguajes o charcas (charca) fueron seleccionados en cuatro sitios: dos en la pradera de Festuca cerca de Stavely en el sudoeste de Alberta, uno en la pradera mixta en Onefour en el sudeste de Alberta y uno en la pradera de Palouse cerca de Kamloops en la Colombia Británica. Vaquillas de un año fueron utilizadas en tres sitios y pares de vacas con terneros en un sitio de Stavely. En cada sitio, tres potreros salieron en forma radiada de la charca conteniendo diez vaquillas de un año o diez vacas con terneros al pie, asignadas al azar al agua limpia (agua llevada a un bebedero de un pozo, un río, o una charca), agua de la charca bombeada a un bebedero (charca bebedero), o acceso directo a la charca (charca directo). Los estudios fueron repetidos en cada sitio de 3 a 6 años. Se realizaron observaciones de aumentos de peso del ganado, el espesor de la grasa del lomo de las vacas y vaquillas y el tiempo que pasaron en diferentes actividades. Fueron analizadas muestras fecales de parásitos y patógenos seleccionados. Otros estudios fueron conducidos para determinar los efectos del agua contaminada con abono en la consumición del pienso y del agua y la selección del agua. Los terneros, con las vacas bebiendo el agua limpia, ganaron un 9% más ($P < 0.10$) de peso que aquellos con las vacas en charca directo, pero el peso de las vacas y el espesor de la grasa del lomo no fueron afectados. Las vaquillas de un año que tenían acceso al agua limpia ganaron un 23% ($P = 0.045$) y un 20% ($P = 0.076$) más de peso que aquellas en charca directo y charca bebedero, respectivamente. El ganado evitó el agua que estaba contaminada con 0.005% de abono fresco de peso cuando tenía acceso al agua limpia. El ganado que tenía acceso al agua limpia pasó más tiempo pastando y menos tiempo descansando que el que fue ofrecido el agua charca directo o el agua charca bebedero. Los administradores del ganado deben considerar la calidad del agua junto con las condiciones del forraje para lograr la producción óptima de la pradera.

Key Words: ponds, dugouts, weight gains, water intake

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On rangeland, water for cattle is commonly derived from dugouts, ponds, or wells. Water quality is affected by its source and contamination from abiotic and biotic factors as a result of either dissolved nutrients or direct deposition of urine or fecal material containing nutrients and possibly parasites. Cattle are commonly hosts to *Giardia* spp., *Cryptosporidium* spp., nematodes and others parasites that affect their health. Giardiasis causes diarrhea in calves and lambs (Olson et al. 1995), *C. parvum* affects young calves (Olson et al. 1997a), and *C. muris* affects older animals (Anderson 1991). Water from deep wells or springs may have a high salt content if it originates from marine shales while dugouts and ponds are recharged mostly from surface water runoff or ground water that contains variable amounts of dissolved nutrients.

The effects of salt on cattle or sheep performance have been extensively studied. High salt content reduced sheep performance possibly by increasing osmolality of the rumen contents which suppressed feed intake (Barrio et al. 1991). Weeth and Capps (1972) reported no reduction in water intake by young cattle with SO_4 levels up to 2,814 ppm added as Na_2SO_4 . However, feed intake was reduced at the 2,814 ppm SO_4 level and growth rate was reduced at the 1,462 ppm SO_4 level or higher. Concentrations of 3,493 ppm SO_4 reduced feed intake and resulted in weight loss in cattle (Weeth and Hunter 1971). Other studies reported tolerances of cattle to SO_4 concentrations up to 4,732 ppm but water intake was depressed by 20% at concentrations of 6,760 ppm (Embry et al. 1959).

Nutrient loading in dugouts also promotes the growth of algae that affect water quality by causing eutrophication and, more seriously, poisoning when toxic blue-green algae are present. There are several genera of algae that belong to the group commonly referred to as toxic blue-green algae. They include *Anacystis*, *Anabaena*, *Aphanizomenon*, *Nodularia*, and *Oscillatoria* and are associated with 2 types of toxins, hepatotoxins and neurotoxins (Beasley et al. 1989). While the toxicity of blue-green algae has been clearly identified, the effect of subclinical doses of these toxins on animal performance and water palatability are still not well defined.

Perhaps the most predictable factor reducing palatability of water is fecal contamination, yet very few studies have examined the effects on water consumption. Holechek (1980) reported a decrease

in water consumption and weight gain of cattle drinking from a water source contaminated with feces and urine. Conversely, Crawford et al. (1996) reported no difference in weight gain of cattle drinking water from a pond to which they had direct access. In a pilot study, we found that cattle drinking from a dugout gained 23% less weight than those drinking clean water delivered to a trough. As a result of this evidence, a study was conducted to examine the effects of water source on cattle production and activity behavior in field experiments, to determine the impact of selected chemical and biological constituents on these observed responses, and to test the effect of fecal contamination on water consumption in penned trials.

Materials and Methods

The effect of water source was tested during the summer in southern Alberta; 2 sites were tested near Stavely (50° 12', 113° 57') in the fescue prairie and 1 at Onefour in the mixed prairie (49° 04', 110° 27'). One additional site was located in south central British Columbia near Kamloops (50° 33', 120° 08'). The Kamloops grasslands were similar to the Stavely site having a dominance of rough fescue (*Festuca campestris* Rydb.). The mixed prairie site was representative of the *Stipa-Bouteloua* faciation of the mixed prairie (Coupland 1961).

Cattle response to water source (field trial)

Two experiments were conducted to determine the effects of water source on performance of Hereford cattle: One examined the effects on yearling cattle (Yearling Experiment) while the second examined the effects on cow-calf pairs (Cow-Calf Experiment). The Yearling Experiment was conducted at 3 sites, repeated in 3 to 5 years (random variable), and had 3 water-source treatments. The sites (with number of trial-years) were at Kamloops (5), Stavely (3), and Onefour (5). The treatments were (1) clean water supplied either from a well, a spring, or a river into a trough, (2) water pumped from a pond or dugout (hereafter referred to as a pond) into a trough (Pond_{trough}) and the pond fenced to prevent access, or (3) direct access by cattle to the pond (Pond_{direct}). Clean water was transported by truck and stored in a 5,500 liter storage tank that was insulated to minimize light and moderate water temperatures. Flow of water from the tank was controlled by a

float valve in the trough. Water for the Pond_{trough} was delivered with an electric pump activated by a depth sensor in the trough. The trials were facilitated with 3 paddocks of equal area, radiating from a pond, and randomly assigned to a treatment in each trial-year. The same ponds and paddocks were used repeatedly over the study period.

The Cow-Calf Experiment was conducted at a second pond at Stavely over 6 years. The arrangement of paddocks and treatments were the same as that for the Yearling Experiment. The treatments were randomized among paddocks each year.

Cattle performance Yearling Experiment

Each paddock was stocked with 10, 16-mo old yearling cattle over a 2-mo period between July and September of each year. Animal size among treatments was harmonized by ranking the 30 test animals by weight and randomly allocating them in groups of 3 among the treatments. Open heifers were used in all years at Onefour and in 2 years at Kamloops and 1 year at Stavely. Steers were used in 3 years at Kamloops and 2 years at Stavely. The trials at Stavely were terminated early, and the data not used in the analyses, when the animals escaped their paddocks in 1996 and insufficient water was available to complete the trial in 1999. The average stocking rates were 2.08, 0.69, and 0.86 animal-unit-month (AUM) ha⁻¹ on sites at Stavely, Onefour, and Kamloops, respectively. The stocking rates were matched with the pasture condition to ensure that forage did not limit cattle production.

Cow-Calf Experiment

Each paddock was stocked with 10 cow-calf pairs for a 2-mo period except in 1994 when 6 pairs were used. The protocol for allocating cow-calf pairs among treatments was the same as for yearlings except that backfat thickness was used to rank the animals. The average stocking rate, since 1994, was 2.96 AUM ha⁻¹. The proportion of male to female calves was maintained constant among treatments to account for differences in growth and demands on the cow. The cows were obtained from the same herd each year and bred for calving in March.

Animal weights were determined at the beginning and end of each trial. At the time of weighing, backfat thickness was measured, for cows only, at the spinal process above the 11th rib on the left side of the animal about 15 cm from the midlines of the vertebrae using a portable

Krautkramer USK 7 ultrasound machine (Krautkramer Branson, Hürth, Germany). Changes in weight and backfat thickness were assessed over the duration of the trial.

Cattle activity

Estimates of cattle activity and drinking times were made with direct observations on the herd and individual animals, respectively, at Stavely (2 sites) and Onefour (1 site), and on individuals at all 4 sites over 2 to 6 years. Thus, both cows with calves and yearlings were observed. The observers positioned themselves at a vantage point from where all 3 paddocks could be seen and drinking times of individual animals could be measured. Individual animals were identified by unique physical or color markings. Thirty, half-hour observations were made simultaneously on herd activity at each water source from dawn to dusk, over 3 to 5 days during 3 years. Herd activity was recorded as grazing intensely, grazing lightly, loafing, resting, or drinking. Grazing lightly was defined as feeding while walking; loafing included socializing and standing while resting involved lying down. Drinking activity was defined as the time committed to obtaining water and includes ingestion and positioning for the purpose of ingesting water. This differs from the observation on individual animals where drinking was defined as actively ingesting water.

Observations on individual animals were focused on estimating time spent ingesting water as an index of volume consumed. Two animals were selected in each treatment for observation, from dawn to dusk over the duration of the sampling period. Drinking times were measured with a stopwatch.

Chemical and biological quality of water

Water samples (250 ml) were collected at the time cattle were weighed from each source by dipping a sterile bottle into water at a depth and place from where cattle would normally drink. The samples were immediately cooled and delivered to a commercial laboratory for analysis of elemental and microbiological constituents. Water quality (chemistry and bacteria) in Alberta was tested by the Trace Elements/Environmental Toxicology Laboratory at the University of Alberta, Edmonton, Alberta. In British Columbia, the analyses were performed by the Pacific Environmental Science Centre

of Environment Canada, Vancouver, British Columbia.

Only pond water was sampled ($Pond_{direct}$, $Pond_{trough}$) for algae in 1998 and 1999 at each site and in 1997 at both Stavely sites. The clean water was not sampled since algae biomass was negligible. At Stavely and Onefour, samples were taken every 2 weeks beginning at the start of each trial while at Kamloops water was sampled 2 weeks after the start and 2 weeks before the end of the trial.

Water was sampled for algae with a plankton net having a diameter of 11.2 cm. The net was drawn at a fixed distance through the water to a depth of 30 cm. In the pond, three, 1.5-m long samples were taken at different locations and composited. A single 60-cm long sample was taken in the trough. Total volume sampled was 45 liters from the pond and 6 liters from the trough. After sampling, the bottles were immediately placed in a cooler in preparation for analysis. Algae were examined and identified to genus according to Clesceri et al. (1989) and reported as cell numbers liter⁻¹. The algae species were classified according to toxic blue-green of the genera *Anabaena*, *Anacystis*, *Aphanizomenon*, *Arthrospira*, and *Oscillatoria* and others (*Ceratium*, *Diatoma*, *Dinobryon*, *Euglena*, *Fragilaria*, *Gomphosphaeria*, *Spirogyra*, *Synedra*, *Tabellaria*, and *Volvox*) that were recognized for reducing palatability for humans through odor or taste (Ingram and Prescott 1954, Palmer 1959).

Statistical analyses

Weight changes in the Yearling Experiment were analyzed as a factorial that included 3 water treatments, 3 sites, years nested in site, and their interactions. For the Cow-Calf Experiment, changes in weight of both cows and calves, and backfat thickness of cows were analyzed as a factorial with sex of calf, 3 water treatments, replication over years, and their interactions. All analyses were evaluated using mixed effects ANOVA (SAS 1999) with year being a random variable. Treatment means were compared using single degree of freedom contrasts.

Observations on herd activity were analyzed in a factorial arrangement that included 3 water treatments, 3 sites, and years ($n = 2$ to 6) nested in site. All analyses were evaluated using a mixed effects ANOVA (SAS 1999) with year being a random variable. Treatment means were compared using single degree of freedom contrasts. Drinking times were estimated

over 4, 6, 3, and 2 years at Stavely (Cow Experiment), Stavely (Yearling Experiment), Onefour, and Kamloops, respectively and analyzed with the same model used for activity.

Role of pathogens and parasites on cattle performance

The potential role of pathogens and parasites in affecting cattle performance was tested by comparing infection rates among water source treatments and between infected and non-infected animals. Rectal faecal samples were taken at the time of weighing both in 1996 and 1997 at 2 Stavely sites (Yearling and Cow Experiments) and at Onefour. The samples were kept refrigerated until analyzed for the presence of *Giardia* spp. cysts, *Cryptosporidium* spp. oocysts, and nematode eggs.

Analysis of *Giardia* and *Cryptosporidium* spp.

Fecal suspensions were squeezed and filtered through 4 layers of NuGauze (Johnson and Johnson, Montreal, Canada) to yield 7 ml of filtrate. The filtrate was layered over 5 ml of 1 M sucrose (specific gravity 1.13) and centrifuged at 800 x g for 5 min to concentrate the cysts at the sucrose/water interface. The interface and upper layer of liquid were transferred by pipette to a clean tube and recentrifuged (800 x g for 5 min). The supernatant was decanted and the pellet was suspended in sodium phosphate buffered saline to a volume of 1 ml.

Two, 0.015-ml samples of the concentrate were spotted on microscope slides and allowed to air dry on a slide warmer for a minimum of 30 min. Once dry, the slide was fixed with acetone, dried, and mixed with 20 μ l of either *Giardia* or *Cryptosporidium* fluorescein isothiocyanate labeled monoclonal antibody solution (Giardi-a-glo, Crypt-o-glo, Waterborne, New Orleans, La). The sample was then incubated in a humidity chamber at 37° C for 30 min. After incubation, slides were rinsed with phosphate buffered saline and the slide was left to air dry. Once dry, slides were mounted with glycerol (Aqua-polymount, Polysciences, Warrington, Penn.) and a cover slip and examined using an epifluorescent microscope at 200 x and 400 x magnification. The number of cysts (*Giardia*) and oocysts (*Cryptosporidium*) over the spotted area were counted and subsequently the number of cysts or oocysts per gram of feces was calculated. Oocysts of *C. muris* were differentiated

from those of *C. parvum* based upon their spherical size and shape 6.6-7.9 Fm x 5.3-6.5 Fm, ovoid for *C. muris*; 4.5-5.4 x 4.2-5.0 Fm, spherical for *C. parvum*). Oocysts and cysts from all samples were identified and enumerated by the same individual and previously established positive and negative control fecal samples were analyzed with each sample lot. The immunological reagents have been shown to be specific for *Giardia* spp. cysts and *Cryptosporidium* oocysts (Xiao et al. 1994, Olson et al. 1997b) with a sensitivity of 67 cysts/oocysts gram⁻¹ of feces.

Analysis of Nematodes

Ova of parasitic nematodes and cestodes were enumerated using a modification of the technique described by Cox and Todd (1962). Five gram samples of feces were diluted with 22 ml of 2.5% potassium dichromate solution, filtered through 2 layers of cheesecloth, and centrifuged for 10 min at 5,000 x g. The pellet was resuspended in a saturated sugar solution and centrifuged at 5,000 x g for 10 min. The eggs on two, 22 x 22 mm cover-slips were identified and enumerated. Eggs of *Nematodirus* spp., *Trichuris* spp. and *Monenzia* were identified. Eggs of other trichostrongyle genera could not be differentiated and were identified as "trichostrongyle."

Statistical analysis

Analyses were made to determine (1) whether the water sources had an effect on infection rates of the cattle and (2) whether weight gains were related to infection. Since counts of organisms or eggs does not reliably estimate their degree of impact on the animal, the comparison in the first analysis was based on the number of animals infected by the specific organism and, in the second analysis, on the weight gain of animals infected versus non-infected by the specific organism. In each case, infection was determined by the presence or absence of the organism, identified by genus, in the fecal sample. Analyses were made for *Giardia* spp., *Cryptosporidium* spp., "trichostrongyle" spp., and *Nematodirus* spp. Presence or absence of the remaining organisms were not sufficiently balanced to permit a meaningful comparison.

The effect of water source on infection was based on the final fecal sample taken at the conclusion of the trials and analyzed as a factorial using a mixed effects ANOVA (SAS 1999) model with year (n = 2) the random variable. The fixed factors were 3 sites and 3 water treatments

and their interaction. The effects of infection on weight gain were analyzed by pooling animals across water source treatments and analyzing their weight gain as a factorial using a mixed effect ANOVA (SAS 1999) model with year (n=2) being the random variable and fixed factors of 2 infection treatments, 3 sites, and their interaction. Replication was achieved by individual animals.

Effect of fecal contamination on water consumption (penned trials)

Two experiments were conducted to determine cattle response to manure contamination in penned trials. In each experiment, manure was collected fresh at the beginning of each trial from a nearby pasture and refrigerated in an air-tight container to be used as required. Water was offered in 140-liter water troughs, constructed from tires, and having the water intake at the bottom and designed to stir the water and mix the sediments as the animal was drinking. This would simulate the effect of an animal walking into a pond and disturbing the muck. The flow of water into the trough was controlled with a float valve and was metered to determine daily consumption. Manure was added at the beginning of each trial and then daily in amounts proportional to water consumption.

Sixteen-month old yearling steers were used in each experiment. Before every trial, the animals were brought into a holding area and fed cubed alfalfa hay and offered clean water from a well. The same hay and water was offered to the animals during the trials with the only exception being the rates of manure contamination.

Effect of contaminants on water selection

The effect of manure contamination on water selection was tested with choices of 3 concentrations (0, 0.05, and 0.25 mg manure gram⁻¹ water) and 4 replications. Three troughs spaced about 1-m apart were arranged in a row at one end of the pen and treatments were allocated randomly for each replication. Eight steers were randomly assigned to 4 groups of 2 animals each and allocated among replicates. The replications were run consecutively over 7 days each.

Effect of contaminants on water and feed intake

The effect of manure contamination on water and feed intake was examined in 2 trials, each designed in a 4 x 4 Latin

square with 4 treatments, 4 pens, and 4 times. Each time consisted of observations over 10 days that were repeated consecutively after changing the assigned treatment in each pen according to design. For the analyses, the observations were divided into 2, 5-day periods with the first representing a conditioning period. Eight steers were randomly allocated into 4 groups of 2 animals each and assigned to a pen for the duration of the trial. The 4 treatments in Trial 1 were concentrations of manure at 0, 0.05, 0.15, and 0.45 mg · gram⁻¹ water and in Trial 2 the concentrations were 0, 2.5, 5.0, and 7.5 mg gram⁻¹ water. Different animals were used between trials and the hay was weighed in and out each day to determine feed intake.

Statistical analysis

The water selection study was analyzed as a split plot design with an unstructured error matrix using a mixed effects model (SAS 1999). This allowed the analyses of day since trial initiation, and its interaction with treatment, as a repeated measure and permitted a more detailed examination of the daily adjustment by the animals to the treatments. The main effects were 3 water contamination treatments and 7 days of exposure. The water contamination treatment was tested by its interaction with replication. Day since trial initiation and its interaction with treatment was tested by the residual. As a result of a significant ($P = 0.004$) interaction of water treatment and day, selection in each day was analyzed separately and the means compared with single degree of freedom contrasts.

The effects of contaminants on feed intake by 2 animals were analyzed for both periods. Average water and feed intakes for each period were determined and analyzed using ANOVA (SAS 1999) for each trial separately. Treatment means were compared using single degree of freedom contrasts. The relationship between water and feed intake was evaluated with a simple linear regression across treatments and periods for each trial (SAS 1999).

Results

Cattle response to water source (field trial) Chemical and biological quality of water

Well water had more Na, CaCO₃, and SO₄ than water from ponds at Stavelly and Onefour (Table 1). The concentration of salt, as measured by conductivity (Fs cm⁻¹), from well water was greatest at Onefour. Pond water at Kamloops had concentra-

Table 1. Chemical characteristics and coliform counts ($\bar{x} \pm 1$ SE) in water offered to cattle at 4 sites.

Site	Treatment	pH	Conductivity ($\mu\text{S} \cdot \text{cm}^{-1}$)	Na (mg $\cdot \text{liter}^{-1}$)	K (mg $\cdot \text{liter}^{-1}$)	Ca (mg $\cdot \text{liter}^{-1}$)	CaCO ₃ (mg $\cdot \text{liter}^{-1}$)	NO ₃ + NO ₂ (mg $\cdot \text{liter}^{-1}$)	Sulphate (mg $\cdot \text{liter}^{-1}$)	Total TDS ¹ (mg $\cdot \text{liter}^{-1}$)	Faecal Coliform (no. $\cdot 100\text{ml}^{-1}$)	Coliform (no. $\cdot 100\text{ml}^{-1}$)
Canadian Water Quality Guidelines (1999)												
Stavely - c ² (1995 - 98)	n=11, yr=5 Clean ³	8.50	1032	227	2.35	24	365	0.20	181	675	177	108
		0.04	44	19	0.17	3	5	0.04	16	32	92	83
	n=11, yr=5 Pond	7.87	347	4	8.71	42	169	0.06	3	177	279	233
		0.06	15	0.3	0.76	3	7	0.00	1	7	124	39
Stavely - y ⁴ (1995 - 99)	n=7, yr=4 Clean ³	8.51	1027	228	2.26	22	362	0.13	183	673	8	6
		0.05	56	19	0.13	2	12	0.02	14	36	4	2
	n=8, yr=4 Pond	8.41	356	6	7.33	32	177	0.05	10	185	257	149
		0.11	28	2	0.84	4	19	0.00	2	19	166	10
Onefour - y	n=5, yr=4 (1994 - 99) Clean ³	8.76	3296	826	4.84	13	684	0.06	1046	2324	15	4
		0.05	673	176	0.34	1	42	0.00	312	379	6	7
	n=2, yr=2 (1998 - 99) Clean ⁵	8.17	225	8	1.0	21	92	0.05	14	110	4	4
		—	—	—	—	—	—	—	—	—	—	—
	n=7, yr=6 Pond	8.83	250	24	8.37	16	115	0.06	5	31	93	58
		0.33	13	5	0.84	1	7	0.00	1	11	32	25
Kamloops - y (1995, 98 - 99)	n=1, yr=1 1995 Clean ⁶	7.78	2408	132	27.00	127	875	0.05	765	1783	24	24
		—	—	—	—	—	—	—	—	—	—	—
	n=4, yr=2 1998 - 99 Clean ⁵	8.46	95	2	1.37	13	36	0.01	6	—	35	16
		0.24	2	0	0.11	0	1	0.00	0	22	9	—
	n=5, yr=3 Pond	9.00	9596	1276	142.50	70	836	0.00	5900	—	531	182
		0.04	3002	431	60.62	10	100	0.00	2292	—	63	62

¹Total dissolved solids.

²Denotes trial with cow-calf pairs.

³Clean water taken from a well.

⁴Denotes trial with yearling cattle.

⁵Clean water taken from a river.

⁶Clean water taken from a spring.

tions of SO₄ that varied from 7,900 to 18,000 mg liter⁻¹ from July to September, respectively, in 1998 and from 1,440 to 3,810 mg liter⁻¹ from May to September, respectively, in 1999. A single sample measured in August 1995 had 2,600 mg

liter⁻¹ SO₄. Water sampled from all sites had NO₂ + NO₃ levels that were well below toxic levels for cattle (Table 1). Clean water from all sources had fewer coliforms than water from ponds.

Toxic blue-green algae were present at

all sites at concentrations up to 7.5×10^6 cells liter⁻¹ (Table 2). Other algae genera capable of producing odours or unpleasant taste for humans were also present in mostly lower concentrations than those detected for the toxic algae.

Table 2. Average algae densities ((cells · liter⁻¹)⁻¹⁰⁰⁰) at biweekly intervals over the trial periods at Stavely and Onefour and near the beginning and end of trials at Kamloops in pond water offered by direct access or in a trough.

Algae Genera	Cow-calf												Yearling							
	Stavely						Stavely						Onefour				Kamloops			
	1997		1998		1999		1997		1998		1998		1999		1998		1999			
	Direct	Trough	Direct	Trough	Direct	Trough	Direct	Trough	Direct	Trough	Direct	Trough	Direct	Trough	Direct	Trough	Direct	Trough		
n	5	4	4	4	3	3	10	4	4	3	4	3	3	3	2	2	2	2		
Toxic blue-green																				
<i>Anabaena</i>	13	8	12	10	4		17	12	134	24	3	2	22	35	1		255	8		
<i>Anacystis</i>		4	10	2	101	41	3	8	1	8	T ²	15	143	77			142			
<i>Aphanizomenon</i>	T	T	T	1			8	2	T		T	2	T							
<i>Arthrospira</i>	17	10					2				2									
<i>Oscillatoria</i>	66	36	192	18	19	12	28	13	47	4	19	35	91	11	6	1	10			
Total	109	193	258	31	12	61	7582	1791	230	35	374	1858	315	123	7	1	406	8		
Other¹																				
<i>Ceratium</i>	T	1	3	1	33	37	12	12	T	T	T	T	3	2	1	T				
<i>Diatoma</i>	2	2	35	16	1	T	2	1	22	119	10	11	T	T	66	1141	6	2		
<i>Dinobryon</i>			1						1	1					T					
<i>Euglena</i>	T	T	T	T			1	T	T		T				T	1				
<i>Fragilaria</i>	1	11	3		T	1	66	7	37	12	T	1	T		1	1	9	1		
<i>Gomphosphaeria</i>	T		34	2	2	2	3		2		1		T	T						
<i>Spirogyra</i>	372	9	6	10	4		4	3	18	201	1	1	18	7	7		21	11		
<i>Synedra</i>					T												T			
<i>Tabellaria</i>																	2			
<i>Volvox</i>	T	T					384	T												

¹All genera represent algae that can affect palatability to humans through odour or taste.

²Trace - less than 1 (cells · liter⁻¹)⁻¹⁰⁰⁰.

Table 3. Effect of water supply on weight and backfat thickness of cows¹, and weight gains of calves¹ and yearlings² over 3 to 6 years.

Water treatment	Cows		Calves	Yearling			
	Weight	Back fat	Weight	Overall ¹	Stavelly	Onefour	Kamloops
	(kg • day ⁻¹)	(mm)	(kg • day ⁻¹)	-----	(kg • day ⁻¹)		
years (n)	6	6	6		3	5	5
Clean (1)	0.60	0.92	1.17	0.79	0.77	0.65	0.95
Pond							
Trough (2)	0.48	0.90	1.14	0.66	0.68	0.54	0.76
Direct (3)	0.53	1.16	1.06	0.64	0.73	0.51	0.69
SEM	0.09	0.28	0.06	0.09			
Effect (P)	>0.10	>0.10	>0.10	0.090			
Comparisons	-----Probability-----						
1 vs 2	>0.10	>0.10	>0.10	0.076			
1 vs 3	>0.10	>0.10	0.056	0.045			
2 vs 3	>0.10	>0.10	>0.10	>0.10			

¹The interaction of calf sex, or its interaction with treatment, was not significant ($P > 0.10$) for weight or backfat thickness in cows; weight gains in calves was affected ($P = 0.004$) by sex; the interaction of sex x treatment was not significant ($P > 0.10$).

²The site x treatment interaction was not significant ($P > 0.10$).

Cattle performance

Clean water produced 23 and 20% greater ($P < 0.10$) weight gains, among yearling cattle, than pond_{direct} or pond_{trough}, respectively (Table 3). The effect was similar ($P > 0.10$) across sites but less evident at Stavelly (Table 3). Weight gains in relation to water source was not consistent among years. The greatest deviation from the average trend was a 3.7% greater gain on pond_{direct} than from clean water at Kamloops in 1995 (Data not shown).

The effect of water source treatment on weight gains of cows with calves was not significant ($P > 0.10$) although average weight gains were 13 and 25% more for cows drinking clean water than from pond_{direct} or pond_{trough}, respectively (Table 3). Backfat thickness also was not responsive ($P > 0.10$) to water treatments

(Table 3) and calf sex had no effect ($P > 0.10$) on weight or backfat thickness (Data not shown). Calves on clean water gained more weight than calves having direct access to pond water ($P = 0.056$) while pond water pumped to a trough produced intermediary results ($P > 0.10$, Table 3). Male calves gained more ($P = 0.004$) weight than female calves (1.18 vs 1.07 kg • day⁻¹; data not shown).

Cattle activity

Cattle offered clean water spent more time grazing ($P = 0.002$) and less time resting ($P < 0.001$) and loafing ($P = 0.029$) than cattle drinking directly from the pond (Table 4). Drinking activity and drinking times were similar ($P > 0.10$) among treatments. Activity behaviors were similar ($P > 0.10$) among treatment at each site

Table 4. Budget of cattle activities and drinking times in relation to water source at several sites over 2 to 6 years at each location¹.

Water treatment	Grazing	Resting	Loafing	Drinking activity ²	Drinking time ³
	----- 30 min. increments-----			---- (sec • day ⁻¹) ----	
Clean	18.1	8.3	1.0	1.4	77
Pond					
Trough	16.5	9.5	1.6	1.2	80
Direct	15.7	9.8	2.3	1.0	85
SEM	0.7	0.2	0.2	0.1	3
Source	-----Probabilities-----				
Site (1)	>0.10	>0.10	>0.10	>0.10	<0.001
Treatment (2)	0.002	<0.001	0.029	>0.10	0.316
1 x 2	>0.10	0.048	>0.10	>0.10	0.985
Treatment Comparisons					
1 vs 2	0.007	<0.001	>0.10	>0.10	>0.10
1 vs 3	0.001	<0.001	0.010	>0.10	>0.10
2 vs 3	0.091	0.089	>0.10	>0.10	>0.10

¹Activity budgets were estimated at 2 Stavelly sites (cow-calf and yearling) and at Onefour over 3, 2, and 2 years respectively; drinking times were estimated at 2 Stavelly sites (cow-calf and yearling), at Onefour and at Kamloops over 6, 4, 3 and 2 years, respectively.

²Time that is committed to obtaining water; includes drinking and positioning for the purpose of drinking.

³Time that is spent ingesting water; the mouth is in contact with the water surface.

except for resting at Stavelly where clean = pond_{trough} < pond_{direct} and at Onefour where clean < pond_{trough} = pond_{direct}.

Role of pathogens and parasites in cattle performance

Infections by *Giardia*, *Cryptosporidium*, *Trichostrongylus*, or *Nematodirus* spp. were similar ($P > 0.10$) among water treatments and sites. Animal weight gains were not affected ($P > 0.10$) by infection as indicated by the presence of the organisms tested in the feces (Table 5).

Effect of fecal contamination on water consumption (penned trials)

Cattle tended to avoid water that was contaminated by 0.05 mg fresh manure • g⁻¹ water, preferring to consume water without manure when given a choice (Table 6). This effect was consistent in each day of the trial except on the first day when they drank similar ($P > 0.10$) amounts of clean water and water contaminated with 0.05 mg manure • gram⁻¹ water. However, when a single choice was offered, water consumption was depressed only at manure concentrations above 2.5 mg • gram⁻¹ water while feed consumption was depressed at concentrations greater than 5 mg • gram⁻¹ water (Table 7). The relationship between feed intake and water consumption was expressed by the equations: Feed_{kg} = 6.2 kg + 0.16 kg • liter⁻¹ for Trial 1 ($r^2 = 0.78$, $P < 0.001$); and Feed_{kg} = 13.6 kg + 0.04 kg • liter⁻¹ for Trial 2 ($r^2 = 0.20$, $P < 0.001$). The response represents a ratio of about 6 and 25 liter water • kg⁻¹ dry matter consumed in Trials 1 and 2, respectively.

Discussion

Effect of water source

The effects of pond water on weight gains among yearling cattle were similar among a diverse range of sites but considerable differences existed among years for both cows and yearlings (Table 3). Because the response was measured relative to clean water, the yearly treatment response is a function of acceptance or avoidance of both sources. As such, errors of interpretation could be introduced from the lack of an unsuitable control. Clean water obtained from wells at Stavelly and Onefour had higher concentrations of salt than water from ponds although they were within the acceptable limits (Table 1). However, the criteria defining water quality that explained cattle performance were not likely estimated by the chemical or

Table 5. Weight gains of cows (with calves) and yearling cattle over a 2-month period in relation to infection (No - absent; yes - present) by *Giardia* spp., *Cryptosporidium* spp., and gastrointestinal nematodes ('trichostrongyle'), and *Nematodirus* spp. at 2 sites over 2 years. The effects of *Trichuris* and *Monezia* spp. infection on weight gains are not shown².

	<i>Giardia</i> spp.		<i>Cryptosporidium</i> spp		'trichostrongyle'		<i>Nematodirus</i> spp.	
	No	Yes	No	Yes	No	Yes	No	Yes
Stavely (cow-calf pair)								
n	45	14	36	23	42	17	12	47
Wt. gain (kg)	33	37.3	29.4	41.2	34.5	32.8	36.3	33.5
Stavely (yearling)								
n	38	21	37	22	43	16	2	57
Wt. gain (kg)	31.6	35.3	33.5	31.9	32.1	35.1	32	32.9
Onefour (yearling)								
n	41	19	53	7	50	10	17	43
Wt. gain (kg)	15.5	14.8	15.2	15.9	15.6	13.7	13.9	15.8
Overall Effect ¹								
Wt. gain (kg)	26.7	29.1	26	29.6	27.5	29	22.9	27.4

¹The effect of infection, or its interaction with site, was not significant ($P > 0.10$) for any specific parasite.

²*Trichuris* and *Monezia* spp. were present in 9 and 87%, of all animals, respectively.

biological parameters measured but rather were defined by organic compounds that affected smell or taste (with the possible exception of 1 year at Kamloops when very high levels of SO_4 were observed).

The response of cows to water treatments was likely reflected in the weight gains of their calves who receive a major portion of their nutrition from milk. Greater milk production contributes to faster growth in calves but at the expense of the dam (Taylor 1994).

Pumping water and excluding cattle from the pond appeared to produce immediate results over the relatively short period of the study but could conceivably produce more convincing benefits in the long-term. Although the Pond_{trough} treatment produced results that were most similar to Pond_{direct}, their ranking tended to be intermediate to clean water and Pond_{direct} suggesting that cattle might prefer drinking from a trough and avoid entering the pond. This suggestion is supported by longer grazing times on Pond_{trough} than Pond_{direct}, with the assumption that grazing times are positively correlated with water consumption. Calves seemed to benefit the most by exclusion from the pond although their performance is also linked to their dams. Excluding cattle from direct access to the pond could be expected to produce greater benefits over the long-term through improved water quality as direct fouling is halted and the riparian vegetation is allowed to recover and filter nutrients.

Proposed mechanism of cattle response

The detrimental effect of pond water on weight gains of cattle appears to be mediated through feed intake rather than by stress induced by pathogens, toxins, or

parasites. Cattle that drank clean water spent longer time grazing and, in penned studies, ingested more feed. Therefore, the proposed mechanism to explain weight gain response to water source appears to be defined by the palatability of water that influences water and forage consumption. Pond water was less palatable than clean water, which resulted in less water and feed intake and reduced animal performance. While the trends for average drinking times (Table 4) did not support the contention that more clean water was consumed than pond water ($P > 0.10$), the discrepancy may be explained by variable rates of water intake, among treatments, defined by palatability. However, the hypothesis that intake rates are affected by palatability needs to be tested. In at least 1 year at Kamloops, a high SO_4 content appeared to be responsible for reduced weight gains.

Water intake from ponds and feed intake from pastures were not measured but the greater time spent grazing by cattle having clean water suggests greater feed intake as the forage characteristics among paddocks were similar at each site. The relationship

between water consumption and feed intake has been established (Hyder et al. 1968). The fluid matrix within the rumen plays a key role in facilitating microbial attachment to feed particles and their subsequent digestion (McAllister et al. 1994). Butcher et al. (1959) reported a ratio of 3 liter water for each kg dry matter of feed consumed when the temperature was about 5° C and 7 liter when the temperature was 32° C. Utley et al. (1969) reported a reduction in feed intake from 6.2 to 4.8 kg day⁻¹ when water was restricted to 60% of free choice. The ratios of water to feed also decreased from 2.9 to 2.2 liter kg⁻¹. In the present study, the ratios averaged 3.8 and 4.3 liter • kg⁻¹ in Trials 1 and 2, respectively. However, the response of feed intake to water consumption, defined by the regression coefficients of the equations, was considerably greater in Trial 1 than in 2 (6 vs 25 liter • kg⁻¹). Trial 1 was conducted when the average daily temperature was lower than during Trial 2 (13.6 vs 16.1° C, data not shown) and thereby imposing relatively greater demands for cooling than for rumen function.

Table 6. Water selection by 2 yearling steers in relation to contamination with fresh manure over the duration of the trial (n = 4)¹.

Manure conc.	Days from trial initiation						
	1	2	3	4	5	6	7
(mg • g ⁻¹ water)	-liters $\bar{x} \pm \text{SEm}$ -						
0	68 (24)	124 (12)	106 (32)	118 (14)	116 (14)	102 (19)	86 (10)
0.05	53 (27)	13 (12)	27 (22)	19 (12)	16 (9)	22 (18)	38 (10)
0.25	1 (1)	0 (0)	8 (5)	4 (2)	10 (3)	21 (6)	16 (4)
Effect (P)	0.138	<0.001	0.047	0.001	<0.001	0.017	0.003
Comparisons	-Probabilities -						
0 vs 0.05	>0.10	0.001	0.095	0.002	0.002	0.025	0.014
0 vs 0.25	0.071	0.002	0.054	0.004	0.004	0.021	0.003
0.05 vs 0.25	>0.10	>0.10	>0.10	>0.10	>0.10	>0.10	>0.10

¹The interaction of treatment x day was significant ($P = 0.004$)

Table 7. Effect of manure-contaminated water, at a high and low range of concentrations, on water and feed consumption by 2 yearling steers over 2 consecutive, 5-day periods (n = 4).

Manure conc.	water	feed	water	feed
(mg • g ⁻¹ water)	Conditioning period		Test period	
Trial 1 (low)	(liters)	(kg)	(liters)	(kg)
0	110	28	127	33
0.05	112	29	119	33
0.15	112	30	127	34
0.45	116	30	128	34
SEM	6	1.1	4	0.7
Effect (P):	>0.10	>0.10	>0.10	>0.10
Trial 2 (high)				
0	152	30	154	32
2.5	123	31	148	31
5.0	107	30	113	30
7.5	112	27	124	28
SEM	13	0.5	5	0.8
Effect (P):	>0.10	0.022	0.003	0.068
Comparisons:				
0 vs 0.25	>0.10	>0.10	>0.10	>0.10
0 vs 0.50	0.046	>0.10	0.001	>0.10
0 vs 0.75	0.073	0.009	0.005	0.013
0.25 vs 0.50	>0.10	>0.10	0.002	>0.10
0.25 vs 0.75	>0.10	0.006	0.021	0.083
0.45 vs 0.75	>0.10	0.027	>0.10	>0.10

Potential palatability factors

The specific compounds responsible for reducing water palatability are unknown although Dohi et al. (1999) identified organic fractions in cattle feces that appear to be responsible for causing avoidance. It is purely speculative that these fractions were also present in pond water. However, cattle were observed to walk into the pond to drink and often defecated while standing in the water. Of 78 observed drinking incidences by cows at Stavely 26% resulted in defecation into the pond (Data not shown).

Assuming an animal produces 25 kg manure fresh weight daily, defecates 10 times a day, and defecates 25% each time it drinks from the pond (on average of twice a day), each animal would then contaminate an equivalent volume of 25,000 L per day with 0.05 mg fresh manure • grams⁻¹ water. This is further aggravated within the pond environment by repeated contamination in the shallow part of the pond. Cattle would avoid this concentration of manure if given a choice of clean water (Table 6).

The role of algae in affecting cattle performance in this study is unclear but might contribute to reduced palatability and can be toxic. The effect of algae on water palatability has not been tested but the toxicity of some species to cattle has been clearly established. Symptoms in cattle are weakness, variable hyperthermia, reduced responsiveness, anorexia, mental derangement, shock, and death (Beasley et al. 1989). While lethargy may be an early symptom of toxicity, and might explain

reduced grazing and greater resting times of animals drinking from the pond, algae densities did not appear to affect performance. For example in 1997 at Stavely, yearling cattle performed similarly while drinking pond water directly or from a trough (Table 3) although algae densities in the trough were only about 25% of the density in the pond (Table 2). Similar evidence exists in 1998 at both Onefour and Kamloops when algae densities were above average and varied between water treatments, but weight gains of cattle between treatments were similar.

Salt concentrations in water were clearly implicated as a factor affecting cattle weight gains at Kamloops in 1998 when SO₄ concentrations greatly exceeded 8,000 mg • liter⁻¹, a concentration that depressed water intake by 20% (Embry et al. 1959). Cattle drinking pond water had diarrhea and displayed symptoms of salt overload. Salt concentrations in the pond water are determined by recharge and evaporative losses. As a result, concentrations tend to increase over the summer and vary among years in relation to the weather.

Conclusion

Clean water is essential for maximizing cattle weight gains on rangeland in summer. Over a 2-month period, yearling cattle gained 23% more weight when drinking clean water than drinking directly from a pond and 20% more than drinking

pond water pumped to a trough. Calves with dams gained 10% more weight. It is not clear how these effects would translate to the production cycle of cattle through compensatory growth and different water sources as the animals' environment will change. For producers that sell their cattle in fall, the opportunity for benefitting from potential compensatory gains is clearly lost to the buyer.

The study raises a number of questions that need to be addressed in further research. One is on compensatory growth as discussed above. A second question is on the secondary effects of preventing direct access on water quality and the riparian environment. Here the specific issues are on the nature and stability of anti-palatability factors in water and the function of riparian zones. The nature of exclusion itself needs to be examined as ranchers are unwilling to fence off the pond from cattle in the event of a pump failure. Therefore, the third question is on the effectiveness of offering water offsite in preventing direct access to the pond and damage to the riparian zone. Finally, the fourth question is on the application of the results to non-pasture environments such as feedlots where cattle are subject to an environment with high manure concentrations.

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Influence of grazing lease terms on economic optimal stocking rates

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Abstract

The terms of grazing lease contracts potentially influence a tenant's incentive to preserve the vegetation resource. Annual stocking rate decisions dictate the degree of overgrazing, which can be cumulative over long periods of time. The objective of this study was to identify the impact the tenant's lease length and lease type has on profit maximizing stocking rates. A multi-period nonlinear programming model was developed to identify economically optimal stocking rates each year over a 24-year period. The model was solved under 1-, 4-, 8-, and 12-year leases on a "per ha" and "per head" basis. The relative importance of each lease alternative and other input values in explaining the tenant's optimal stocking rate was ranked based on standardized ordinary least squares coefficient estimates. Lease length and lease type had a minor impact on optimal stocking rates relative to non-lease factors such as livestock prices and production costs. Holding lease length constant, per ha leases generated a 2% higher average stocking rate than per head leases. Optimal stocking rates were inversely related to the length of the lease. Twelve-year leases generated 18 and 13% lower optimal stocking rates than the 1-year per ha and per head leases, respectively. The optimal stocking rate difference between an 8-year and a 12-year lease was negligible, suggesting the 8-year lease would provide a similar incentive to protect vegetation as a lease with a longer planning horizon.

Key Words: Lease Type, Lease Length, Standardized Beta Coefficient

Alternative lease arrangements influence soil and vegetation protection incentives faced by agricultural producers. Overgrazing is a common cause of declining ecological condition on rangeland and pasture (Ellison 1960). Stocking rate, defined as the number of animals on a given land area for a fixed period of time, is the primary decision variable management can use to control overgrazing. Profit-maximizing stocking rates may vary depending on the livestock operator's property rights associated with the land. The type and duration of grazing leases impact tenant stocking rate incentives by influencing the planning horizon, and/or the cost structure of the grazing enterprise.

Length of the Lease

The length of the planning horizon often is cited as an important factor in the livestock producer's incentive to stock appropri-

Resumen

Los términos de los contratos de arrendamiento de pastoreo influyen potencialmente el incentivo del arrendatario por conservar el recurso vegetación. Decisiones del rango del inventario ganadero anual dictan el grado de sobre pastoreo, el cual puede ser acumulativo sobre largos periodos de tiempo. El objetivo de este estudio fue identificar el impacto que la duración del arrendamiento así como el tipo de arrendamiento tienen en la maximización de ganancias de los rangos de inventario ganadero. Un modelo de programación no lineal de multiperiodo fue desarrollado para identificar rangos de inventario económicamente óptimos cada año en un periodo de 24 años. El modelo fue resuelto bajo 1-, 4-, 8-, basándose en "por hectárea" y "por cabeza" durante 12 años de arrendamiento. La importancia relativa de cada alternativa de arrendamiento y otros valores al explicar el rango optimo de inventario del arrendatario fue clasificada basada en estimaciones estandarizadas de los coeficientes de los cuadrados mínimos ordinarios. Duración del arrendamiento y tipo de arrendamiento tuvieron un impacto menor en los rangos óptimos de inventario relativos a factores no relacionados con el arrendamiento como precios del ganado y costos de producción. Manteniendo la duración del arrendamiento constante, arrendamiento por hectárea generó un 2 % mas en promedio que el arrendamiento por cabeza. Rangos óptimos de inventario fueron relacionados inversamente a la duración del arrendamiento. Doce años de arrendamiento generaron 18 y 13 % rangos óptimos de inventario menores que el arrendamiento de 1 año por hectárea por cabeza, respectivamente. La diferencia del rango optimo de inventario entre arrendamientos de 8 y 12 años fue insignificante, sugiriendo que el arrendamiento por 8 años proveería un incentivo similar para proteger la vegetación que el de un arrendamiento con un horizonte de planeación más amplio.

ately (Torell et al. 1991, Workman 1986). The length of a grazing lease may represent the planning horizon for land operated by a tenant with uncertain lease renewal prospects. Relatively short leases, therefore, may encourage tenants to overstock and exploit the forage resource for short-term profitability at the expense of long-term pasture productivity. A short-term planning horizon, however, does not guarantee that a tenant will have an economic incentive to overgraze. Because individual weight gain decreases as stocking rate increases, excessive stocking can reduce profitability, even with a single year planning period. For example, Launchbaugh (1957) conducted grazing trials near Hays, Kansas, and found that light stocking rates were usually more profitable than heavy stocking rates. Shoop and McIlvain (1971) suggest

producers who overgraze usually are not behaving in their economic self-interest. Workman (1986) suggests overgrazing is usually a result of ignorance and over-optimistic forage production estimates, and occurs in spite of the profit motive, not because of it.

Several studies estimating economic optimal stocking rates suggest livestock operators periodically have an incentive to deplete or "mine" the forage resource. Hart et al. (1988) estimated the profit-maximizing stocking rate near Cheyenne, Wyo., assuming 1986–1987 price/cost conditions, to be 60 to 80% above the Soil Conservation Service (now NRCS) recommended level to maintain range condition. Manley et al. (1997) reported that stocking rates 30 to 75% higher than the NRCS recommended level were profitable during favorable cattle price periods. McCollum et al. (1999) found the most profitable stocking rate under continuous grazing in tall-grass prairie exceeded NRCS recommendations.

These studies used single-period models and did not consider the impact of the current stocking rate decision on future forage production. Evaluating stocking rate incentives under alternative forms of land tenure requires a model that considers the decision maker's relevant multi-year planning horizon. Dynamic optimization models consider the impact of future pasture productivity and profitability by maximizing the sum of the discounted income stream over the relevant time horizon. Pope and McBryde (1984) used a dynamic optimization model to compare the profitability of systematic overstocking coupled with periodic re-vegetation treatments to maintaining a sustainable stocking rate. Optimal stocking rates approached the biological sustainable level as the planning horizon increased to perpetuity. The grazing strategy that maximized the sum of the discounted cash flow streams was to slightly overgraze and deplete the forage over a 10-year planning horizon.

Torell et al. (1991) compared optimal stocking and forage utilization rates for a single period model to an expanded model with a multi-period planning horizon based on Colorado production data (Sims et al. 1976). Profit-maximizing stocking rates were slightly lower in the dynamic (long-term horizon) model relative to the myopic (single-period) model. With variable beef price situations, economically optimal stocking rates were variable and rangeland productivity was not greatly reduced with either a single period or a long term planning horizon. The authors

concluded that inter-temporal impacts on forage production were a relatively minor consideration in the current stocking rate decision. Current period animal performance at alternative stocking rates was the most important consideration in the stocking rate decision.

Cost Structure

Economically optimal stocking rates are influenced by the cost and revenue structure of the grazing enterprise (Hart 1991, Workman 1986). The grazing lease type (per head or per ha lease payments) influences the cost structure of the grazing enterprise, and, consequently, profit-maximizing stocking rates. Cost structure refers to the proportion of total costs categorized as fixed or variable. Fixed costs do not change with the level of production. Examples of typical fixed costs include interest, insurance, and depreciation. Variable costs change with the level of production. Typical variable costs in a livestock operation include feed, veterinary care, animal care, and other costs that change with the number of head.

When lease contracts specify compensation on ha basis, lease payments are fixed costs with respect to stocking rate. In this situation, total lease costs are unrelated to the stocking rate. Tenants operating under this type of lease can reduce per-head costs by increasing stocking rates. The

tially a public issue as excessive grazing can impact aesthetic values, noxious weed encroachment, and downstream water quality. Furthermore, tenant operators manage a substantial portion of Kansas grazing lands. These externalities create a public interest in whether certain lease contracts systematically encourage overgrazing. Promoting lease terms that reduce tenant incentive to overgraze may be an effective method of addressing these issues. The objective of this study was to explore the relationship between alternative lease types common to grazing land and economically optimal stocking rates. This relationship is then compared to the impact of non-lease influences such as livestock prices and production costs.

Methods

Nonlinear programming models were used to estimate the optimal stocking rate on Kansas Flint Hills pasture each year over a 24-year period under 2 alternative lease types (per ha and per head) and 4 alternative lease lengths (1, 4, 8, and 12 years). The model combined livestock prices, lease rates, and production costs observed each year from 1975–1998. The objective function of each model was specified as follows:

$$\text{Max } \pi_k = \sum_{t=1}^k [\text{HD}_t * (\text{OSP}_t * \text{OSW}_t - \text{MSP}_t * \text{MSW}_t - \text{VCH}_t - \text{LRH}_t) / (1 + r)^t] \quad (1)$$

$$\text{Max } \pi_k = \sum_{t=1}^k [(\text{HD}_t * (\text{OSP}_t * \text{OSW}_t - \text{MSP}_t * \text{MSW}_t - \text{VCH}_t) - \text{LRA}_t * 260) / (1 + r)^t] \quad (2)$$

level of fixed costs does not affect the stocking rate decision in the short run but all costs must be covered in the long run (Workman 1986).

Lease payments are a variable cost (per ha) when the lease calls for compensation on a per head basis. In this situation, total lease costs are directly related to stocking rates. The profit-maximizing stocking rate occurs where the additional (marginal) revenue generated by each additional animal equals the additional (marginal) cost. Given diminishing marginal productivity as animals are added to the pasture, profit maximizing stocking rates are reduced as the per head lease rate increases. Conversely, stocking rate in the per ha lease type does not affect the lease component of marginal costs. This implies per ha leases may encourage tenants to stock heavily relative to per head leases.

Management of private pasture is poten-

Equations 1 and 2 represent the objective functions for the per head (hereafter denoted head lease) and per ha lease (hereafter denoted ha lease) models, respectively. The decision variable in each model is the number of head (HD_t) stocked on a full section (260 ha) pasture each year. The symbol π_k represents cumulative pasture profitability over the length of the lease. Cumulative pasture profitability is evaluated on a per section basis regardless of the leased type or lease length evaluated. The symbols MSW_t and OSW_t represent to May steer weight and October Steer Weight, respectively. For this study, MSW was assigned a constant value of 270 kg every year and OSW is determined by Equation 3. The remaining symbols, MSP_t and OSP_t , represent May Steer Price and October Steer Price, respectively.

$$\text{OSW}_t = \text{MSW}_t + \text{DOP}_t * \text{ADG}_t; \quad (3)$$

The model based future stocking rate decisions on expected rather than actual livestock prices. Table 1 shows the

Table 1. Method of modeling price expectations in a 4-year lease.

Decision year	Solved for years			
	1	2	3	4
1	A	B	B	B
2		A	B	B
3			A	B
4				A

A = The stocking decision was based on the actual observed May steer price, and a basis adjusted futures price for the October steer price.

B = The stocking decision was based on 5-year moving average cash prices for both May steer price and October steer price.

method of modeling price expectations over multi-year leases using a 4-year lease as an example. In the first year of the lease, the model determined stocking rates for years 1 through 4. In year 2 of the lease, the model was solved for years 2 through 4 based on new price information observed in year 2 and vegetative conditions inherited from the previous year. In the third year, the model was solved for years 3 and 4, while in the fourth year, the model was solved for year 4. The model moved on to the next lease period and repeated this process based on new price expectations and vegetative conditions inherited from the previous lease period. This method allowed the model to allocate the effects of the current stocking rate decision over the relevant planning horizon based on expected long- and short-term cattle prices.

Price expectations used in the model were formed using May and October Dodge City, Kansas, feeder cattle prices from 1975 through 1998. Price expectations for the October steer price in the 1-year models, and year t in the multi-year lease models, were basis adjusted October futures prices observed in May. Price expectations for both May and October steer prices for years $t+1$ through k of the multi-year lease models were based on 5-year moving average cash prices. All price and cost data were expressed in nominal dollars.

Calf prices typically decrease as the weight of the animal increases (Dhuyvetter and Schroeder 2000). This trend, referred

to as the weight price slide, was approximated with a linear interpolation between prices of 315 and 360 kg steers observed each year (Dhuyvetter¹ and Schroeder 2000, Mark et al. 2000). The model used the average price slide of $\$-0.04$ (100 kg)⁻¹ observed over the study period. For each kilogram increase in October steer weight, the October steer price decreases by $\$0.04$ (100 kg)⁻¹.

Operating costs incurred in the model are normally incurred on a per head basis. Operating cost estimates were taken from Kansas summer stocker budgets compiled by Jones and Dhuyvetter (1999), and include interest on purchased livestock, veterinary care, labor, mineral, and miscellaneous costs. A continuous operating cost data series was not available for the relevant time period. Nominal costs, therefore, were assigned to each year by inflating Jones and Dhuyvetter (1999) estimates using the producer price index. Interest on purchased livestock was calculated from operating loan rates observed each year and reported by the Federal Reserve Bank of Kansas City (1975–1998).

Equations 3 through 7 express the relationships that limit the optimal stocking rate. In Equation 3, the coefficient DOP_t refers to the days on pasture in year t and was assigned a constant value of 150 days. Equation 4 defines average daily gain (ADG) in year t .

$$ADG_t = 1.00 - 0.0029 * GP_t \quad (4)$$

The linear function was taken from Torell et al. (1991) but coefficient values were recalibrated to match weight gains observed at various stocking rates in the Kansas Flint Hills tallgrass region (Smith and Owensby 1978, Launchbaugh and Owensby 1978). A linear relationship between stocking rate and ADG is supported by research over a wide range of

geographic locations (Hart 1972, 1993, Jones and Sandland 1974, Manley et al. 1997). Specifying average daily gain as a linear function of grazing pressure implies livestock gain ha^{-1} is a quadratic function of stocking rate. The models, therefore, have a non-linear objective function.

Figure 1 shows the per head and per ha stocking rate weight gain response functions derived from Equation 4. These functions assume forage production levels of 3,600 kg ha^{-1} . The inverse relationship between stocking rate and weight gain $head^{-1}$ limits the economic incentive to overgraze. Maximum weight gain per head at very low stocking rates was approximately 150 kg over the entire grazing season, representing an average daily gain of 1.0 kg. Maximum weight gain per ha was approximately 30 kg at a stocking rate of 260 head for the grazing season. Reducing the forage production assumption shifts the curves downward but does not change the slope.

Equation 5 defines grazing pressure in year t (GP_t) as stocker days per unit of available standing herbage (Hart et al. 1988). Available forage (AF_t), represented in Equation 6, is a function of pasture forage production capacity (FPC) and the herbage production index in year t (HPI_t). Pasture FPC was exogenously assigned the equivalent of 3,600 kg ha^{-1} (Launchbaugh and Owensby 1978).

$$GP_t = HD_t * DOP_t / AF_t \quad (5)$$

$$AF_t = FPC * HPI_t \quad (6)$$

The herbage production index in year t (HPI_t) expressed in Equation 7 provides the link between past grazing pressure and current forage production.

$$HPI_t = 0.4343 + 0.5824 HPI_{t-1} - 0.00136 GP_{t-1} \quad (7)$$

Fig. 1. Functional relationship between stocking rate and weight gain on a per head and per ha basis.

¹Dhuyvetter and Schroeder (2000) found a non-linear price slide over a relatively extreme range of cattle weights. For the weight range relevant to this study, however, a linear price slide was a close approximation.

Ranging between zero and one, HPI_t values represent the proportion of forage production capacity available for grazing in year t . The functional form and coefficient values were derived from Torell et al. (1991). Specifying HPI_t as a function of the previous year grazing pressure and HPI suggest HPI_t is an implicit function of all past grazing pressure levels.

The model determined the optimal stocking each year considering impacts on future forage production through the remainder of the lease period. Future income was discounted at the nominal rate of 11.5% per year. This rate represents the average operating loan rate over the 24-year study period reported by the Federal Reserve Bank of Kansas City (1975–1998).

The lease rates assigned to each period were regional averages taken from the Bluestem Pasture Report (Kansas Agricultural Statistics Service 1975–1998). For example, the lease rate assigned to the first period of the 4-year model was the average lease rate observed from 1975–1978. The lease rate for the second 4 years was the average rate observed between 1979–1982. This pattern applied to all lease models.

Head leases were modeled in this study as a mixed cost structure, rather than a strict variable lease cost. Multi-year lease contracts, by definition, guarantee a minimum annual payment for the duration of the lease. Consequently, even per head lease payments would realistically have a fixed cost component as a tenant may be under a contractual obligation to make lease payments based on some pre-specified stocking rate. A landlord would unlikely accept a tenant wishing to pay for very few head. This suggests a tenant would face some minimum lease payment with a value independent of the number of head actually stocked.

The next issue in setting minimum lease payments in the head model was identifying what stocking rate should the minimum lease payment be based. In the Kansas Flint Hills, landowners offering per head leases guarantee a minimum land area per head (Kansas Agricultural Statistics 1975–1998). The acreage guarantee varies from year to year based on vegetative and market conditions, and this value is reported annually in the Bluestem Pasture Report (Kansas Agricultural Statistics 1975–1998). The reciprocal of the acreage guarantee observed each year was considered an approximation of the minimum stocking rate dictated by the grazing lease market. In the model, the

tenant was obligated to pay for at least the number of head the acreage guarantee would suggest, but was to free stock the pasture at any level. Lease costs increased linearly by the head lease rate for stocking rates greater than the level established by the acreage guarantee.

Sensitivity Analysis

The relative importance of lease type, lease length, livestock prices, and production costs in the stocking rate decision was ranked based on standardized ordinary least squares regression coefficients estimated using the models represented in Equations 8 and 9.

$$HD_t^* = f(LENGTH_t, TYPE_t, VC_t, MSP_t, OSP_t) \quad (8)$$

$$HPI_t^* = f(LENGTH_{t-1}, TYPE_{t-1}, MSP_{t-1}, OSP_{t-1}) \quad (9)$$

The dependent variable HD_t^* denotes the optimal stocking rate values generated each year by the models represented by Equations 1 and 2. The dependent variable HPI_t^* denotes the herbage production index value generated by Equation 7 at each HD_t^* . The independent variables in Equations 8 and 9 were input values used by models 1 and 2 to generate each HD_t^* observation. The variable $LENGTH$ denotes the lease length used to generate each observation of HD_t^* , assuming a discrete value of 1, 4, 8, or 12 years. Lease type ($TYPE$) was a binary variable assigned a value of 0 if the lease was specified on a per head basis, and a value of 1 if the lease was specified on a per ha basis. The variable VC_t denoted variable operating costs observed each year, while MSP_t and OSP_t represent May steer price and October steer price, respectively. Since HPI_t is a function of previous year grazing pressure and herbage production index, the independent variables in Equation 9 were all lagged 1 year. The variable VC_t was omitted from Equation 9 because of confounding trends in the data. Models 8 and 9 each had 156 observations, 24 years model⁻¹ times 8 models (2 lease types times 4 lease length alternatives).

Standardizing estimated coefficients entails scaling ordinary least squares coefficient estimates by the ratio of the standard deviation of the relevant independent variable to the standard deviation of the dependent variable (Pindyck and Rubinfeld 1998). This calculation converts ordinary least squares estimates to unit-free coefficients whose absolute magnitudes are directly comparable, revealing the relative impact of the independent variables on the dependent variable.

Simply put, this technique reveals how many standard deviations the dependent variable is expected to change in response to a standard deviation change in each respective independent variable (Mark et al. 2000, Featherstone et al. 1997).

Parametric analysis was used to examine the sensitivity of the model to other input variables that could potentially affect the results. Inter-temporal vegetative condition responses to grazing pressure would potentially influence the relationship between planning horizon and the current stocking rate decision. This relationship was incorporated into the model through Equation 7. The coefficient values in Equation 7 were estimated from data collected in eastern Colorado (Sims et al. 1976). These values may depend on regional growing conditions and, therefore, may not accurately represent eastern Kansas. Parametric analysis was used to identify the sensitivity of the results to changes in the coefficients. Each model was solved after changing coefficient and constant values, one term at a time, to 80 and 120% of the original estimates.

To compare leases with alternative time horizons, future income flows should be discounted to present value. Discounting places a greater value on income received in the near future relative to the distant future, increasing the incentive to mine the forage. The rate at which future income is discounted may impact the stocking rate decision. The discount rate, however, may not have a significant impact on optimal stocking rates if price/cost conditions frequently do not favor exceeding the steady state grazing pressure. Sensitivity of average optimal stocking rates to the discount rate was evaluated by comparing the results at alternative discount rates.

Results

Optimal Stocking Rates

Table 2 shows the optimal number of head stocked on the pasture each year under head and ha lease types. The average number of steers stocked on the 260 ha pasture in the 1-year ha lease scenario was 144 head, while the solution for the 4-, 8-, and 12-year leases were 130, 124, and 122, respectively. The head lease type reveals a similar trend. The average number of steers stocked was 136, 131, 123, and 120 head in the 1-, 4-, 8-, and 12-year leases, respectively.

As the length of the lease increased, average optimal stocking rate decreased. The largest decrease in the ha lease type

Table 2. Optimal number of head stocked in a full-section pasture each year under alternative lease agreements.

Year	Per Hectare Leases				Per Head Leases			
	1-Year	4-Year	8-Year	12-Year	1-Year	4-Year	8-Year	12-Year
	Head Per Section (260 ha)							
1975	218	135	122	122	156	235	203	196
1976	238	223	215	215	152	62	36	35
1977	221	221	204	203	152	152	152	152
1978	137	152	121	120	145	231	145	145
1979	167	156	173	171	157	108	122	117
1980	128	110	118	110	139	139	139	139
1981	160	161	160	142	142	142	142	134
1982	103	116	119	66	125	145	145	105
1983	113	68	63	87	125	49	60	70
1984	147	123	113	135	145	145	145	145
1985	155	159	144	166	142	107	89	112
1986	110	125	62	128	119	172	145	181
1987	106	64	80	59	110	145	145	145
1988	108	80	88	68	110	128	139	120
1989	134	123	129	99	135	149	149	139
1990	109	123	125	70	110	140	144	102
1991	121	89	85	98	122	56	54	56
1992	134	104	92	99	134	152	152	152
1993	112	103	84	87	113	112	81	81
1994	144	159	127	129	144	98	74	71
1995	162	131	145	146	149	149	149	149
1996	141	102	108	109	144	156	156	156
1997	139	142	145	145	143	117	126	125
1998	142	161	162	163	141	55	57	57
Average	144	130	124	122	136	131	123	120

occurred when the lease increased from 1 to 4 years, while the largest increase in the head lease type occurred between the 4- and 8-year leases. In both head and ha leases, the optimal stocking rate difference between 8- and 12-year leases was minimal. Average stocking rate in the 1-year ha and head lease agreements was 22 and 16 head greater than the corresponding 12-year lease agreements. This represents an 18 and 13% difference in optimal stocking rates between the extreme lease length scenarios included in the study. Furthermore, there was a large degree of year-to-year variability in optimal stocking rates with all lease arrangements, corresponding largely to the variation in annual beef prices used in the analysis.

The ha lease type generated an average profit-maximizing stocking rate similar to the head lease type. Removing the landlord imposed minimum lease payment, however, substantially reduced the optimal stocking rate in the head lease type. Solving the 1-year model using a strictly variable head lease type reduced the average optimal stocking rate to 91 head section⁻¹. This represents a 33 and 37% reduction in average optimal stocking rates relative to the original head and ha models. Furthermore, solving the 1-year model based on a strictly variable per head lease generated a lower optimal stocking rate than the long-term leases with a fixed cost component.

Vegetative Conditions

Figures 2 and 3 show the profit-maximizing herbage production index time path under each lease type. The 1-year ha lease maintained a herbage production index (HPI) value strictly lower than all other alternatives. A clearly dominant lease strategy does not emerge from the data as the lines cross frequently. In general, the HPI time path is inversely related to the stocking rate. Average HPI values, therefore, increased with the length of the lease, but were similar across lease type, consistent with the stocking rate observations. Mean HPI values were 0.66, 0.73,

0.75, and 0.76 in the 1-, 4-, 8-, and 12-year ha leases, and 0.71, 0.71, 0.75, and 0.76 in the 1-, 4-, 8-, and 12-year head leases, respectively.

All grazing leases examined in this study periodically reached optimal grazing intensities that reduced herbage production index (HPI) levels. The 1-year ha lease achieved the lowest herbage production index value for all models considered in the study, 0.54 observed in 1982. This index value suggests that economically optimal stocking rates reduced forage production to 54% of its capacity. Lease type impact on HPI values appears to decline as the lease length increases. Mean HPI values were five percentage points higher in the head relative to the ha lease type, but equivalent in the 8- and 12-year leases.

Factors Influencing Optimal Stocking Rates

Figure 4 graphically illustrates, in decreasing order of importance, the relative impact of cattle prices, production costs, lease type, and lease length in the profit-maximizing stocking rate, based on standardized coefficient values from the regression. Cattle prices were the most important factors influencing optimal stocking rates. For each standard deviation in livestock purchase and selling prices above the mean, optimal stocking rates decrease by 1.327 and increase by 1.169 standard deviations, respectively, from its mean. As expected, variable operating costs were inversely related to stocking rates. All variables included in Figure 4, except lease type, were statistically significant ($p = 0.05$). The R^2 value of 0.289 was relatively low. This value, however, was robust over a variety of functional forms, suggesting specification error is not likely.

Fig. 2. Optimal HPI time path under alternative ha lease agreements.

Fig. 3. Optimal HPI time path under alternative head lease types.

Grazing lease terms modeled in the study, lease type and lease length, were the lowest-ranked factors explaining the variability in the tenant optimal stocking rate. Regression results suggest that holding other variables in Equation 8 constant, the ha lease type increased optimal stocking rates by an average of 2 head section⁻¹ relative to the head lease. In addition, the length of the lease had a relatively minor impact on optimal stocking rates. These results suggest expected short-term livestock price/cost margins and the stocking rate weight gain trade-off carry a larger influence on current optimal stocking rates than expectations regarding future forage production.

Factors Influencing HPI Values

Figure 5 shows the impact of cattle prices, and lease terms on estimated herbage production index (HPI) values. Since HPI values are inversely related to

stocking rate (Equation 5), factors influencing stocking rates could also be expected to influence HPI values. Figure 5 supports this expectation. The ranking was similar to the stocking rate value factors illustrated in Figure 3. The signing of the coefficients, however, was opposite. The October steer price had the greatest impact on herbage HPI with a standardized coefficient value of -1.731, followed by May steer price with a value of 1.498. Lease length and lease type carried the lowest impact on optimal stocking rates, with standardized coefficient values of 0.409 and -0.029, respectively. Consistent with Figure 4, all variables except lease type were statistically significant ($p = 0.05$).

Parametric Analysis Results

The discount rate apparently does not have a large influence on the optimal stocking rate. Reducing the discount rate from 11.5 to 6% reduced average optimal

stocking rate by 1, 2, and 2 head section⁻¹ in the 4-, 8-, and 12-year ha lease types, respectively. The discount rate reduction had a similar impact on the head lease type, reducing optimal stocking rate by 0, 1, and 1 head section⁻¹ in the 4-, 8-, and 12-year models, respectively.

Adjusting the coefficient values in Equation 7 affects optimal stocking rates and herbage production index values, but not the relative importance of lease terms and livestock prices. In all cases, rankings were consistent with the base results shown in Figures 2 and 3. Of the 3 terms in Equation 7, previous year herbage production index had the greatest impact on optimal stocking rates.

Discussion and Conclusions

Understanding the interaction between economic incentives and long-term physical impacts on grazing land is an important component for addressing management-induced pasture deterioration. Expected livestock price/cost margins emerged as the most important factors in the stocking rate decision. This result may diminish the opportunity for landlords, public agencies, or other stakeholders to indirectly address vegetative condition by promoting grazing leases of specific length or type. A landlord wishing to maintain a minimum vegetative condition may need to directly specify appropriate stocking rates in the lease.

Effect of Lease Length

Although livestock prices and operating costs clearly play a dominant role in the stocking rate decision, short-term pasture leases may promote heavier stocking rates than long-term leases. As the length of the lease increased, the optimal stocking pattern appears to approach that of an owner-operator with a perpetual planning horizon². The 24-year lease model generated results similar to the 12-year lease model. Furthermore, optimal stocking rates in the 12-year lease were only slightly lower than the 8-year lease. These results suggest that, holding lease type constant, an 8-year lease would provide a stocking rate incentive similar to a land tenure alternative providing a perpetual planning horizon.

Fig. 4. Relative impact of each input variable on profit-maximizing stocking rates ($R^2 = 0.289$). Standard errors are in parentheses.

²The models were solved assuming an owner-operator land tenure arrangement (essentially an infinite planning horizon). The average profit maximizing stocking rate over the 24 year time period was 121 head section⁻¹.

Fig. 5. Relative impact of each input variable on HPI values ($R^2 = 0.450$). Standard errors are in parentheses.

Range scientists typically define "proper" stocking rates as a level that will maintain or improve ecological condition (Ohlenbusch and Watson 1994, White and McGinty 1992, Launchbaugh and Owensby 1978). By this definition, all land tenure alternatives examined in this study periodically provided an incentive to overgraze. Herbage production index values in each model declined rapidly from the initial value of 1, and converged to a steady state ranging between 0.60 and 0.80. The initial rapid decline in herbage production index values presented in Figures 2 and 3 may not be realistic. Studies suggest vegetation impacts are more gradual. For example, Manley et al. (1997) showed no difference in production among heavy, moderate, and very light stocking rates on mixed-grass prairie after 13 years of grazing. After 18 and 19 years of grazing, however, forage production under heavy grazing was 54 and 69% of that under moderate, and very light grazing, respectively. Equation 7, therefore, may overestimate the rate of decline in herbage production in the initial years.

Although statistically significant herbage production index (HPI) value differences were observed among alternative lease length scenarios, the differences may not be substantial in terms of actual forage production. The mean difference in the HPI values between the 4- and 12-year ha models was 3 percentage points, or approximately 115 kg of forage ha^{-1} . The spread between mean HPI values in the 1-year and 12-year per head lease models was 5 percentage points, or 180 kg of forage ha^{-1} . The 1-year ha lease maintained an HPI value substantially lower than all other lease alternatives considered in the

study. Mean HPI values in the 1-year ha lease model were 10 and 7 percentage points lower than the 12-year and 4-year ha lease models, amounting to approximately 250 kg of forage ha^{-1} . This spread was robust over all coefficient values examined in the parametric analysis of Equation 7.

Herbage production index values appeared to be cyclical, following the beef price cycle. Furthermore, cases where vegetative conditions improved under one lease agreement while deteriorating under another were rare, supporting the hypothesis that stocking rates and subsequent herbage production values were primarily driven by livestock price cycles and production costs, not by future forage production concerns. This conclusion is consistent with Torell et al. (1991) suggesting inter-temporal impacts on forage production carry a minor impact on the optimal stocking rate decision.

Lease Type

Lease type had a relatively small impact on the optimal stocking decision, particularly in the long-term leases. This result can be attributed to the method of modeling lease costs in the per head model. Imposing a minimum lease payment effectively created a mixed variable/fixed cost structure faced by the tenant. At optimal stocking rates below the minimum, the cost structure in the head lease type was identical to that of the ha lease type. Since price/cost margins usually maintained stocking rates below this point, stocking rate incentives were similar across lease types. This study demonstrated, however, that relaxing the required minimum lease payment and converting fixed costs to

variable costs reduces the profit-maximizing stocking rate. This suggests pasture lease market conditions or other circumstances that force tenants into lease contracts that require minimum lease payments increase optimal stocking rates.

Limitations of the Study

This study was based on forage production and price/cost conditions observed in the Kansas Flint Hills. These results may not be applicable to other geographical areas. Inter-temporal impacts of the stocking rate decision vary depending on regional soil conditions and climate. Inter-temporal impacts predicted by the model are based on the coefficient values of Equation 7, which were estimated in eastern Colorado (Sims et al. 1976). The Flint Hills grassland appears capable of recovering quickly from overgrazing relative to rangeland in more arid regions. For example, adjusting Equation 7 to increase the vulnerability of the vegetation to overgrazing may be required to model inter-temporal stocking rate impacts on desert rangelands in the southwestern United States. In this fragile, dry environment, grazing impacts on future forage production may be a much more important consideration than what this study suggests for the Flint Hills of Kansas, or Torell et al. (1991) found in eastern Colorado.

This study was intended to identify the economic incentives confronting landlords and tenants, not necessarily to describe actual behavior. Actual behavior depends largely on the perceptions and objectives of the livestock operator. These results assume perfect knowledge of current stocking rate decision impacts on future grazing capacity. Furthermore, this model assumes a profit-maximization objective. Livestock producers have many objectives other than profit (Torell et al. 2001).

Our models did not account for the impact of precipitation and temperature variation on forage availability. Model results, therefore, should be interpreted as "holding weather conditions constant." Actual forage production and vegetation conditions are affected by the weather. Additional research could focus on how incorporating weather risk would affect the results. In addition, the results of this study clearly reveal that profit-maximizing stocking rate behavior results in multi-year cyclical optimal stocking rate behavior. Future research needs to further examine the interface between cattle cycles and stocking rate economic incentives.

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Free-choice grazing of native range and cool-season grasses

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Abstract

A grazing system which allows cattle to select a season-long diet more nearly meeting their nutrient requirements should facilitate optimal weight gains. A study was conducted near Mandan, N. D. comparing season-long weight gains of yearling steers free-choice grazing on composite pastures containing equal sized plots of 'Nordan' crested wheatgrass (*Agropyron desertorum*) (Fisch. Ex. Link) Schult.), 'Rodan' western wheatgrass (*Pascopyrum smithii* (Rydb.) Löve), 'Lincoln' smooth brome grass (*Bromus inermis* Leyss.), and native range, to pastures containing the individual pasture types alone. The study was initiated in mid-May and terminated in early October each year from 1995–1997. Pastures were grazed at a stocking rate of 1.9 ha per steer for 147 days or 1.7 AUM ha⁻¹. Steer behavior on composite pastures was recorded every 10 min. from dawn to dusk 2 days per week each summer. In 1997, forage samples were clipped for chemical analysis at 4-week intervals from all pasture types either within composite pastures or as individual pasture types. Only in 1996 were daily gains of steers on the free-choice treatment different ($P < 0.10$) from all other treatments. Over the 3-year study, daily gains for steers on the free-choice treatment (1.11 kg) were statistically equal to steers on smooth brome grass (1.04 kg) and western wheatgrass (1.00 kg) and were significantly greater than daily gains on native range (0.98 kg) and crested wheatgrass (0.97 kg). Steers tended to spend a greater percentage of observation time grazing smooth brome grass than the other 3 pasture types, especially early in the grazing season. The period of maximum grazing preference for the other pasture types was late in the season in 1995 and 1996 for crested wheatgrass, in mid-season in 1996 for native range, and late in the season in 1997 for western wheatgrass. Chemical analysis of forage samples collected in 1997 show that smooth brome grass had the highest crude protein and in vitro dry matter digestibility, and the lowest neutral detergent fiber at all 3 summer grazing periods. Forage quality data and the preference of steers for smooth brome grass help to explain why steers on this treatment had excellent daily gains, especially during early and mid-season.

Key Words: animal behavior, crested wheatgrass, western wheatgrass, smooth brome grass

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Resumen

Un sistema de apacentamiento que permite al ganado seleccionar durante largo plazo una dieta muy cercana de llenar sus requerimientos nutricionales debe producir ganancias de peso óptimas. Se condujo un estudio cerca de Mandan, N.D. para comparar las ganancias de peso a largo plazo de novillos en apacentamiento a libre elección de praderas compuestas de parcelas de igual tamaño de "Crested wheatgrass" (*Agropyron desertorum*) (Fisch. Ex. Link) Schult.) variedad 'Nordan', "Western wheatgrass" (*Pascopyrum smithii* (Rydb.) Löve) variedad 'Rodan', "Smooth brome grass" (*Bromus inermis* Leyss.) variedad 'Lincoln' y pastizal nativo contra praderas individuales de las especies anteriores. El estudio se inicio a mediados de mayo y termino a inicios de octubre de cada año durante el período de 1995 a 1997. Las praderas fueron apacentadas con una carga animal de 1.9 ha novillo⁻¹ durante 147 días o 1.7 UAM ha⁻¹. El comportamiento de los novillos en las praderas compuestas se registro cada 10 minutos desde la salida hasta la puesta del sol, estas observaciones se realizaron en el verano durante dos días por semana. En 1997, tanto en las praderas compuestas como en las de especies individuales, se cortaron muestras de forraje para análisis químicos, el muestro fue a intervalos de 4 semanas. Solo en 1996 Las ganancias diarias de peso de los novillos del tratamiento de apacentamiento a libre elección fueron diferentes ($P < 0.10$) del resto de los tratamientos. En el periodo de 3 años del estudio Las ganancias diarias de los novillos en apacentamiento a libre elección (1.11 kg) fueron estadísticamente iguales a las de los novillos apacentando "Smooth brome grass" (1.04 kg) y "Western wheatgrass" (1.00 kg) y fueron significativamente mayores que las ganancias diarias obtenidas en el pastizal nativo (0.98 kg) y en el "Crested wheatgrass" (0.97 kg). Los novillos tendieron a pasar un mayor porcentaje del tiempo de observación apacentando "Smooth brome grass" que en los otros 3 tipos de pradera, especialmente a inicios de la estación de apacentamiento. El período de máxima preferencia para los otros tipos de pradera fue a fines de la estación de apacentamiento de 1995 y 1996 para el "Crested wheatgrass", a mediados de estación en 1996 para el pastizal nativo y a fines de la estación de 1997 para "Western wheatgrass". Los análisis químicos de las muestras de forraje colectadas en 1997 muestran que el "Smooth brome grass" tuvo los mayores porcentajes de proteína cruda y digestibilidad in vitro de la materia seca y los mas bajos de fibra neutro detergente en los 3 períodos de apacentamiento en verano. Los datos de calidad de forraje y la preferencia de los novillos por el "Smooth brome grass" ayudan a explicar porque los novillos en este tratamiento tuvieron excelentes ganancias diarias de peso, especialmente a inicios y mediados de la estación de apacentamiento.

A grazing scheme providing cattle with adequate amounts of high quality forage throughout the grazing season should facilitate optimum season-long performance. Introduced cool-season grasses such as crested wheatgrass (*Agropyron desertorum* (Fisch. Ex. Link) Schult) and smooth brome grass (*Bromus inermis* Leyss.) produce high quality forage that can be grazed much earlier in the spring than native range (Sarvis 1941, Williams and Post 1945). In mid-summer however, when reproductive tillers occur, forage quality and palatability decline (Rogler et al. 1962). If precipitation is adequate for regrowth, crested wheatgrass can also be grazed in the fall (Frischknecht et al. 1953). Total forage production from native range can be increased by deferring its use until mid-June (Campbell 1952).

Grazing systems utilizing seeded cool-season grasses for early season grazing and native range for mid-to-late summer grazing have been proposed by Campbell (1963), Lodge (1963), Currie (1969), and Lorenz (1977) to improve animal performance and enhance the long-term viability of native rangelands in the Northern Great Plains. However, complementary grazing systems require more fencing and increased management to rotate livestock among pastures. Free-choice grazing systems which would reduce these requirements have been proposed by Lodge (1963) and Smoliak (1968). With a free-choice system, ewes tended to rotate themselves among pasture types during the summer and produced weight gains comparable to rotational grazing (Smoliak 1968). The objective of the current research was to determine if weight gains of yearling steers could be improved by season-long free-choice grazing on composite pastures containing equal sized plots of crested wheatgrass, smooth brome grass, western wheatgrass (*Pascopyrum smithii* (Rydb.) Löve), and native range compared to steers grazing these pasture types individually. A secondary objective was to estimate the amount of time steers on composite pastures spent grazing on each pasture type, to facilitate design of better free-choice grazing strategies in the future.

Materials and Methods

Grazing studies were conducted near Mandan, N.D. for 147 days each grazing season from 1995 to 1997. Mandan (46° 46' N, 100° 55' W) has a semi-arid climate with an elevation of 500 m. Grazing periods were from 12 May to 6 October 1995;

10 May to 4 October 1996; and 15 May to 9 October 1997. The study used replicate 24.4-ha composite pastures containing 6.1-ha plots of 'Nordan' crested wheatgrass, 'Rodan' western wheatgrass, 'Lincoln' smooth brome grass, and native range. The native range contained blue grama (*Bouteloua gracilis* (H. B. K.) Griffiths), needleandthread (*Stipa comata* Trin. and Rupr.), green needlegrass (*S. viridula* Trin.), western wheatgrass, sedges (*Carex* spp.), threeawn (*Aristida* spp.) and Kentucky bluegrass (*Poa pratensis* L.). The 6.1-ha plots of the 4 pasture types were used in earlier grazing studies reported by Hofmann et al. (1993) and Karn et al. (1999). In the fall of 1994, following termination of the previous study, replicate composite pastures were established by removing fences which separated adjoining seeded pastures and adjacent plots of native range. Replicate individual 6.1-ha pastures of 'Nordan' crested wheatgrass, 'Rodan' western wheatgrass, 'Lincoln' smooth brome grass and native range were also used. Hence, there were 5 pasture treatments with 2 replications for a total of 10 pastures. The 3 seeded species were established by no-till seeding into spring wheat (*Triticum aestivum* L.) stubble in the fall of 1985 (Hofmann et al. 1993). Pastures were located on fine-silty, mixed, superactive, frigid Pachic Haplustolls and fine-silty, mixed, superactive, frigid Typic Haplustolls soils and had not been fertilized for 10 years before or during the current study.

Composite and individual plots of the 4 pasture types were stocked with 12 and 3 yearling Hereford steers (*Bos taurus*), respectively. Initial steer weights averaged 300 kg. Since composite pastures were 4 times as large as individual pasture type plots, they were stocked with 4 times as many steers to provide an equal stocking rate among treatments. Due to the presence of large exclosures within all treatment pastures the grazing area in composite pastures and individual pasture type plots were reduced to 22.8 and 5.7 ha respectively, which resulted in a stocking rate of 1.9 ha per steer for a 147-day grazing season, or 1.7 AUM ha⁻¹.

Steers were weighed following an overnight stand without feed or water at the beginning and end of each grazing season and at 21-day intervals during the season. Trace mineralized block salt containing 92–98.5% salt, 0.35% zinc, 0.34% iron, 0.20% manganese, 0.033% copper, 0.007% iodine, and 0.005% cobalt was available at all times.

Steer behavior was observed on the 2 composite pastures every 10 minutes from dawn to dusk 2 days each week throughout each of the 3 grazing seasons. For each 10-minute observation period, the location and behavior of the steers were recorded. Behavior was recorded as grazing, standing, lying, scratching, playing, salting, drinking and walking. Observation days totaled 32 in 1995, 34 in 1996, and 38 in 1997. Within a season, data were grouped into early, mid-, and late grazing periods based on seasonal precipitation patterns.

In 1997, forage samples were collected from each pasture type within the composite pastures as well as from the individual pasture type plots at approximately 4-week intervals. Hand clipped samples selected to simulate grazing (Karn and Hofmann 1990) were taken from each pasture by 3 individuals. To insure that pastures were sampled carefully, clippings were taken on 2 consecutive days so that clippers would have time to observe steer grazing patterns and sample accordingly. Collection dates were 29/30 May, 25/26 June, 23/24 July, 20/21 August, and 17/18 September. Following collection, forage samples were dried at 60°C, ground through a 1-mm screen, and analyzed for nitrogen using a Carlo Erba Model NA 1500 series 2 nitrogen/carbon/sulphur analyzer (CE Elantech, Inc., Lakewood, N.J. 08701). Crude protein was calculated by multiplying nitrogen by 6.25. Neutral detergent fiber (NDF), and true in vitro dry matter digestibility (IVDMD) were determined according to Goering and Van Soest (1970). An ANKOM fiber analyzer (Cherney et al. 1997) was used to facilitate measuring NDF in forage samples and forage residue following a 48-hour in vitro fermentation.

Daily precipitation and ambient minimum and maximum air temperatures were recorded at a weather station located 3.2 km north of the study site. Monthly precipitation totals and mean-monthly temperatures (minimum and maximum) were calculated and compared to historic values (Table 1).

Animal weight gain and forage quality data were analyzed using the SAS MIXED procedure (SAS Inst., Inc. 1996) with the replication(treatment) effect considered random. Least squares means were separated by the SAS PDIF option. Animal behavior data were analyzed according to SAS GLM procedures (SAS Inst., Inc. 1985) and pasture type was tested with the replication(pasture type) term. Pasture type means for steer behavior data were separated by the Student-Newman-Keuls' test. Data were considered significant at $P < 0.05$ unless otherwise indicated.

Results and Discussion

Steer performance

Daily gains averaged over the 3 years tended to be higher for steers on the free-choice treatment, but free-choice treatment gains were only significantly ($P < 0.10$) higher than native range and crested wheatgrass (Table 2).

Because of a year by treatment interaction, treatment average daily gains are presented by year as well as 3-yr averages (Table 2). Yearly differences in steer performance were likely related to precipitation amounts and distributions, which in turn affected forage growth patterns. Precipitation levels in 1995 were 52% above the 80-year average (Table 1) and facilitated good forage growth throughout the summer. Steer weight gains in 1995 were above normal for our area and higher than gains in 1996 and 1997. Weight gains were comparable on free-choice and smooth brome grass treatments and the free-choice treatment was significantly higher than western wheatgrass, native range, and crested wheatgrass. In 1996, daily gains on the free-choice treatment were greater ($P < 0.10$) than any other pasture type (Table 2). Adequate early season precipitation (Table 1) facilitated abundant early cool-season forage growth, and above average late season precipitation promoted regrowth of cool-season grasses. Steers on the free-choice treatment had the option of grazing cool-season grasses in the spring and fall and native range in mid-summer, while steers grazing individual pasture types alone had little dietary choice. In 1997, daily gains among pasture treatments were not different ($P < 0.10$). Below average precipitation in May and June 1997 likely reduced early cool-season grass production which was detrimental to steer gain on the free-choice treatment. Observational data suggest that early season grazing pressure was greater on crested wheatgrass and smooth brome grass in the free-choice system,

Table 1. Precipitation (mm) and mean monthly ambient air temperatures (C°) between April and October for 1995-1997 and the 80-year average for Mandan.

	Precipitation				Temperature			
	1995	1996	1997	80-year av.	1995	1996	1997	80-year av.
	----- (mm) -----				----- (C°) -----			
Apr.	30	10	70	43	4	3	4	6
May	173	59	16	57	11	11	12	13
Jun.	66	60	44	75	19	19	20	18
Jul.	152	102	94	60	21	20	23	22
Aug.	43	44	27	49	22	22	21	20
Sep.	30	85	28	41	14	14	16	14
Total	494	360	279	325				

Table 2. Average daily gains $\pm$ SE (kg) of steers grazing free-choice and individual pasture types for 1995, 1996, 1997 and for all 3 years¹.

Treatment	Steers/ treat.	1995	1996	1997	3-yr means
Free-choice	24	1.19 ^a $\pm$ 0.04	1.15 ^a $\pm$ 0.04	1.00 ^a $\pm$ 0.04	1.11 ^a $\pm$ 0.04
Smooth brome grass	6	1.13 ^{ab} $\pm$ 0.06	0.92 ^b $\pm$ 0.06	1.06 ^a $\pm$ 0.06	1.04 ^{ab} $\pm$ 0.04
Western wheatgrass	6	1.05 ^b $\pm$ 0.06	0.95 ^b $\pm$ 0.06	1.02 ^a $\pm$ 0.06	1.00 ^{ab} $\pm$ 0.04
Native range	6	1.07 ^b $\pm$ 0.06	0.92 ^b $\pm$ 0.06	0.95 ^a $\pm$ 0.06	0.98 ^b $\pm$ 0.04
Crested wheatgrass	6	0.96 ^b $\pm$ 0.06	0.91 ^b $\pm$ 0.06	1.05 ^a $\pm$ 0.06	0.97 ^b $\pm$ 0.04
Year LS means		1.12 ^a $\pm$ 0.02	1.04 ^b $\pm$ 0.02	1.01 ^c $\pm$ 0.02	

¹Least squares means within a column among treatments and least squares means by year with different superscripts differ at $P < 0.10$.

because there were 4 times as many steers compared to the individual pasture type plots and steers spent a high percentage of grazing time on these species. Average daily gains for the free-choice treatment over the 3 years were statistically equal to daily gains on smooth brome grass and western wheatgrass and higher ($P < 0.10$) than gains on native range and crested wheatgrass.

Average cumulative weight gains per steer, by weighing period over the 3-year study (Fig. 1), show steers on the free-choice treatment tended to gain less in early and mid-season than steers on smooth brome grass, but in August and September the free-choice treatment had higher daily gains ($P < 0.10$) than steers on smooth brome and crested wheatgrass.

Cumulative weight gains during August and September also improved for steers on individual western wheatgrass and native range treatments and were not different (P

> 0.10) from the free-choice treatment during this period (data not shown). Grazing steers on crested wheatgrass in the spring followed by free-choice grazing on crested wheatgrass and native range during the summer and fall has been reported to be a better system than free-choice grazing on crested wheatgrass and native range for the entire season (Lodge 1963). Perhaps weight gains in the current study could have been improved by grazing smooth brome grass alone early in the season and free-choice grazing on composite pastures the rest of the season. Although early and mid-season weight gain differences between the free-choice and smooth brome grass treatments were small and not significant, it seemed to be a consistent and perplexing phenomena. Perhaps steers on the free-choice treatment voluntarily grazed excessively on lower quality pasture types early in the season, or perhaps our composite pastures with

Table 3. Chemical composition of hand-collected forage samples in treatment pastures, 1997¹.

Pasture type	IVDMD ²			CP ²			NDF ²		
	Early	Mid	Late	Early	Mid	Late	Early	Mid	Late
	----- (%) -----			----- (% of DM) -----			----- (% of DM) -----		
Smooth brome grass	77.0 ^a	71.4 ^a	66.6 ^a	14.0 ^a	14.6 ^a	11.2 ^a	56.1 ^c	61.4 ^c	65.2 ^c
Western wheatgrass	72.5 ^b	67.1 ^b	63.3 ^b	13.6 ^{ab}	13.1 ^b	9.7 ^b	59.3 ^b	65.4 ^b	66.4 ^{bc}
Native range	71.6 ^b	65.7 ^b	61.2 ^b	12.9 ^{bc}	12.2 ^b	8.6 ^c	61.1 ^a	69.1 ^a	68.3 ^a
Crested wheatgrass	72.1 ^b	65.8 ^b	62.8 ^b	12.4 ^c	11.2 ^c	9.7 ^b	58.8 ^b	65.0 ^b	67.1 ^{ab}
SE	0.7	0.7	0.7	0.3	0.3	0.3	0.5	0.5	0.5

¹Least squares means within a column with different superscripts differ ($P < 0.05$).

²IVDMD = in vitro dry matter digestibility, CP = crude protein, NDF = neutral detergent fiber

Fig. 1. Average (1995–1997) cumulative weight gains of yearling steers by weighing period ($\pm$ SE) for free-choice and individual pasture type treatments.

25% smooth brome did not provide enough of this high quality forage to meet steer dry matter requirements.

Forage quality

Statistical analysis of the 1997 chemical composition data for the 4 pasture types indicated an interaction between pasture type and grazing period for NDF and crude protein, therefore data were analyzed by grazing period for all 3 chemical constituents (Table 3). Smooth brome had the highest ($P < 0.05$) IVDMD all three periods and the highest crude protein (CP) during mid- and late season. Smooth brome also had the lowest NDF during early and mid-season. Crested wheatgrass had the lowest mid-season and native range the lowest late season CP. Native range had significantly higher NDF than other pasture types during early and mid-season and was not different ($P > 0.05$) from crested wheatgrass in late season. The expected seasonal decline in forage quality was also evident (Table 3).

Animal behavior

There was a significant pasture type by period by year interaction for grazing behavior, thus data are presented for different pasture types by period and year. In 1995, when precipitation and cool-season grass production was plentiful, steers tended to spend more time grazing smooth brome and crested wheatgrass (Table 4). In the early season, steers spent significantly ($P < 0.10$) more time grazing smooth brome but, by mid- and late

season steers had increased grazing time on crested wheatgrass to equal smooth brome. Steers spent less time ($P < 0.10$) grazing native range and western wheatgrass in the early season. Use of western

wheatgrass appeared to increase from early to late season and was not statistically different than crested wheatgrass the last two periods or smooth brome the final period. Total grazing time as a percentage of observation time increased significantly from early to late season, but grazing time in hours per day ranged from 9.1 to 9.5 hr and was not significantly different among periods (Table 4). Observation time decreased by period as the amount of daylight decreased, thus steers spent a greater proportion of the daylight hours grazing late in the season.

In 1996, steers spent more ($P < 0.10$) time grazing smooth brome than native range in the early period, but in mid-season steers spent about equal time grazing smooth brome, crested wheatgrass, and native range (Table 5). In the late period, grazing time among pasture types was not significantly different. For the full season, grazing time was not different ($P > 0.10$) among pasture types which suggests a more uniform use of all pasture types than in 1995. Grazing time, as a percentage of observation time, again increased progressively during the season, but in 1996, grazing time in hours was

Table 4. Percent of observation time spent grazing pasture types within composite pastures during the growing season of 1995¹.

Pasture type	Early	Mid	Late	Season average
	----- (%) -----			
Crested wheatgrass	15.5 ^b	16.8 ^{ab}	23.7 ^a	18.7 ^{ab}
Smooth brome	20.8 ^a	23.2 ^a	21.6 ^a	22.2 ^a
Native range	8.6 ^c	8.6 ^b	6.5 ^b	8.0 ^b
Western wheatgrass	8.1 ^c	10.1 ^b	13.6 ^{ab}	10.8 ^{ab}
SE	2.9	3.5	3.9	3.0
Total grazing time (%)	53 ^c	59 ^b	65 ^a	60
Total grazing time (hr day ⁻¹)	9.1 ^a	9.5 ^a	9.1 ^a	9.4
Obs. time (hr day ⁻¹)	17.1	16.2	14.0	15.7

¹Early and season-long pasture type means with different superscripts differ at $P < 0.10$ while mid- and late season pasture type means differ at $P < 0.15$. Total grazing time as a percentage and in hours differed among summer periods at $P < 0.05$, and $P < 0.15$, respectively.

Table 5. Percent of observation time spent grazing pasture types within composite pastures during the growing season of 1996¹.

Pasture type	Early	Mid	Late	Season average
	----- (%) -----			
Crested wheatgrass	11.6 ^{ab}	15.0 ^a	19.9 ^a	15.3 ^a
Smooth brome	19.8 ^a	14.3 ^a	14.2 ^a	16.5 ^a
Native range	5.8 ^b	16.1 ^a	16.1 ^a	11.9 ^a
Western wheatgrass	12.7 ^{ab}	10.2 ^b	13.8 ^a	12.5 ^a
SE	2.1	0.7	2.9	1.9
Total grazing time (%)	50 ^c	56 ^b	64 ^a	56
Total grazing time (hr day ⁻¹)	8.4 ^b	8.9 ^a	9.0 ^a	8.8
Obs. time (hr day ⁻¹)	16.9	16.0	14.0	15.7

¹Means within columns among species with different superscripts differ ($P < 0.10$). Total grazing time as a percentage and in hours differed among periods at $P < 0.05$, and $P < 0.15$, respectively.

Table 6. Percent of observation time spent grazing pasture types within composite pastures during the growing season of 1997¹.

Pasture type	Early	Mid	Late	Season average
	------(%)-----			
Crested wheatgrass	16.2 ^b	10.8 ^b	17.5 ^a	15.0 ^b
Smooth brome grass	19.7 ^a	24.7 ^a	14.8 ^{ab}	19.5 ^a
Native range	12.0 ^c	12.1 ^b	10.2 ^b	11.4 ^c
Western wheatgrass	7.0 ^d	11.0 ^b	18.8 ^a	12.6 ^c
SE	1.1	2.2	2.2	0.5
Total grazing time (%)	55 ^c	59 ^b	61 ^a	58
Total grazing time (hr day ⁻¹)	9.1 ^b	9.6 ^a	9.0 ^b	9.2
Obs. time (hr day ⁻¹)	16.6	16.3	14.8	15.8

¹Early, mid- and all season means with different superscripts differ at $P < 0.10$, while late summer means differ at $P < 0.16$. Total grazing time as a percentage and in hours differed among periods at $P < 0.05$, and $P < 0.15$, respectively.

slightly but significantly ($P < 0.15$) lower in early compared to mid- and late season periods (Table 5).

Steers spent the most time ($P < 0.10$) grazing smooth brome grass and the least time grazing native range and western wheatgrass during the early period in 1997 (Table 6). In mid-season, steers spent 25% of the daylight hours grazing smooth brome grass and between 10 and 12% of the time grazing on each of the other 3 pasture types. In the late season, steers spent statistically equal time grazing western wheatgrass, smooth brome grass, and crested wheatgrass, while steers spent less ($P < 0.16$) time grazing native range than crested or western wheatgrass. Total grazing time in hours per day was greatest ($P < 0.15$) in mid-season at 9.6 hours. Although smooth brome grass and crested wheatgrass pastures tended to be favored each year, grazing preference varied by period and year. This variation was undoubtedly related to seasonal changes in plant maturity and forage regrowth patterns. Sheep grazing free-choice season-long on native range, crested wheatgrass, and Russian wildrye rotated themselves among grass species, going first to crested wheatgrass and last to Russian wildrye (Smoliak 1968).

Conclusions

Steers grazing season-long on composite pastures containing equal areas of crested wheatgrass, western wheatgrass, smooth brome grass and native range gained as well as steers grazing only smooth brome grass or western wheatgrass and better than steers grazing native range or crested wheatgrass. Free-choice grazing on composite pastures appeared to improve weight gain in some years more than others, probably depending on the

amount and pattern of precipitation which largely dictated forage growth. Over the 3 years, cumulative weight gains of steers grazing smooth brome grass were highest in early and mid-season while cumulative weight gains of steers on composite pastures were highest in the late season. The cause of this seasonal change is unclear since steers on composite pastures could also graze smooth brome grass. Lodge (1963) alluded to a similar finding with steers grazing crested wheatgrass and native range in Canada. In 1997, smooth brome grass forage quality was greatest in the early season, when steers preferred this grass and produced good weight gains. Although composite pastures used in this study did not consistently produce the highest daily gains, the concept seems valid, and many more combinations of forage types and size of plantings could be incorporated into composite pastures to provide cattle with a more consistent season-long high quality diet.

Over-grazing was not a problem in this research. However, in order to prevent over- or under-grazing, areas of each species need to be seeded according to a projected level of use. Plot size of each species needs to be large enough so that plants can progress through a normal maturity cycle without over-grazing, yet small enough to ensure they will be used before they become too mature. If a forage is readily grazed and matures slowly, then a larger area of that species will need to be used compared to a less palatable forage which matures more quickly. Our experience suggests that if stocking rates are not excessive, determining the proper plot size of each forage species is not difficult. Our data as well as the data of Smoliak (1968) indicate that animals will rotate themselves among pasture types as palatability changes, eliminating the need to fence pasture types separately, and reducing the degree of management required compared to rotational grazing.

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Estimating soil water content in tallgrass prairie using remote sensing

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Abstract

Increased demand for available water supplies necessitates that tools and techniques be developed to quantify soil water reserves over large land areas as an aid in management of water resources and watersheds. Microwave remote sensing can provide measurements of volumetric water content of the soil surface (θ_{vSL}) up to about 10 cm deep. The objective of this study was to examine the feasibility of inferring the volumetric water content of the soil profile (θ_{vBL}) by combining remotely sensed estimates of θ_{vSL} , in situ measurements, and modeling techniques. A simple soil water budget model was modified to estimate θ_{vBL} from assimilated values of θ_{vSL} . Four modeling scenarios were evaluated at 4 tallgrass prairie sites located in central and south central Oklahoma: 1) unmodified model, 2) assimilation of field-measured θ_{vSL} at 2-day intervals, 3) assimilation of field-measured θ_{vSL} matching dates of remote sensing data acquisitions during the study period, and 4) assimilation of remotely sensed θ_{vSL} . The unmodified model (scenario 1) underestimated measurements with root mean square errors (RMSE) between 0.03 and 0.06 $m^3 m^{-3}$ and mean errors (ME) between 0.02 and 0.04 $m^3 m^{-3}$. Model output from scenario 2 agreed well with measurements at all study sites ($|ME| \leq 0.01 m^3 m^{-3}$, $RMSE \leq 0.03 m^3 m^{-3}$). The RMSE and ME values from scenario 3 were comparable to those of scenario 2. Simulations from scenario 4 agreed well with measured data at 2 study sites ($0.00 m^3 m^{-3} \geq ME \geq 0.02 m^3 m^{-3}$, $RMSE \leq 0.03 m^3 m^{-3}$) but underestimated measurements at the remaining sites, in one case by as much as 0.15 $m^3 m^{-3}$. The underestimation was due largely to inaccurate remotely sensed θ_{vSL} values. These preliminary results suggest that it is feasible to infer θ_{vBL} in tallgrass prairies by combining remotely sensed estimates of θ_{vSL} , in situ field measurements, and modeling, provided that the remotely sensed data correctly estimates surface conditions.

Resumen

La creciente demanda del suministro de agua disponible necesita que se desarrollen herramientas y técnicas para cuantificar las reservas de agua en el suelo en grandes extensiones como una ayuda en el manejo de los recursos de agua y las cuencas hidrológicas. Los sensores remotos de microondas pueden proveer de medidas del contenido volumétrico de la superficie (θ_{vSL}) hasta cerca de 10 cm de profundidad. El objetivo de este estudio fue examinar la factibilidad de inferir el contenido volumétrico de agua del perfil del suelo (θ_{vBL}) al combinar las estimaciones de sensores remotos de θ_{vSL} , mediciones in situ y técnicas de modelaje. Un modelo simple de las reservas de agua se modificó para estimar θ_{vBL} a partir de valores asimilados del θ_{vSL} . Se evaluaron cuatro escenarios de modelaje en cuatro sitios de pradera de zacates altos localizados en las regiones central y sur-central de Oklahoma: 1) El modelo sin modificaciones, 2) la asimilación de mediciones de campo del θ_{vSL} a intervalos de 2 días, 3) la asimilación de mediciones de campo del θ_{vSL} concordantes con las fechas de adquisición de datos de sensores remotos durante el periodo de estudio y 4) la asimilación del θ_{vSL} a partir de sensores remotos. El modelo sin modificar (escenario 1) subestimó las mediciones con la raíz de los cuadrados medios de los errores (RCME) entre 0.03 y 0.06 $m^3 m^{-3}$ y los errores medios (EM) entre 0.02 y 0.04 $m^3 m^{-3}$. El modelo resultante del escenario 2 concordó bien con las mediciones en todos los sitios de estudio ($|EMI| \leq 0.01 m^3 m^{-3}$, $RCME \leq 0.03 m^3 m^{-3}$). Los valores de RCME y EM del escenario 3 fueron comparables con los del escenario 2. Las simulaciones del escenario 4 concordaron bien con los datos obtenidos en dos sitios de estudio ($0.00 m^3 m^{-3} \geq ME \leq 0.02 m^3 m^{-3}$, $RCME \leq 0.03 m^3 m^{-3}$) pero subestimaron las mediciones en el resto de los sitios, en un caso por tanto como 0.15 $m^3 m^{-3}$. La subestimación se debió en gran parte a que los valores del θ_{vSL} de los sensores remotos eran inexactos. Estos resultados preliminares sugieren que es posible inferir el θ_{vBL} en las praderas de pastos altos mediante la combinación de estimaciones del θ_{vSL} obtenidas a partir de sensores remotos, mediciones de campo en el sitio y modelaje y que los datos de sensores remotos estimaron correctamente las condiciones de la superficie.

Key Words: hydrology, microwave, water budget

Rangelands comprise over 60% of the land area of the 48 contiguous states, and agricultural, industrial, recreational, and municipal water supplies in many areas of the U.S. are linked directly to rangeland watershed management (Spaeth et al. 1996). An important part of the water budget of any watershed is the amount of water stored in the soil. Although soil water accounts

for only about 0.0001% of the total water on earth, it is a key component in describing the transfer and distribution of mass and energy between the land surface and the atmosphere, it exerts major influences on forage and crop productivity, and it partitions rainfall into runoff and infiltration (Islam 1996). Increased

Fig. 1. Study site locations within the SGP '97 study area.

demand for available water supplies necessitates that tools and techniques be developed to quantify soil water resources over large land areas, such as rangelands, as an aid in management of water resources and watersheds. Equipping watersheds with soil water content measurement sites for routine monitoring is impractical and expensive, especially if the watershed is large or spatially variable in its topography, soil types, and vegetation cover. Remote sensing is a technique that offers potential for providing frequent measurements over large land areas in a timely and cost-effective manner.

Microwave remote sensing can provide measurements of volumetric water content (θ_v) up to about 10 cm deep, depending upon sensor type and wavelength used (Engman and Chauhan 1995). The Southern Great Plains 1997 Hydrology Experiment (Jackson et al. 1999), referred to herein as SGP '97, provides a recent example of attempts to use new microwave technologies to quantify surface soil water content (θ_{vSL}) over large, spatially diverse regions at satellite spatial resolutions. One specific objective of SGP '97, and the objective of this paper, was to examine the feasibility of inferring soil profile water content (θ_{vBL}) by combining remotely sensed estimates of θ_{vSL} , in situ measurements, and modeling techniques (SGP 1997).

Ragab (1995) introduced a simple soil water budget model designed to incorporate θ_{vSL} measurements (in situ or

remotely sensed) to provide estimates of water content within the soil profile. The model requires basic meteorological data and easily obtained soil parameters, which makes it attractive for use in areas where little may be known about the underlying soils. The model was evaluated at 2 short grass pasture sites in England, and found to produce satisfactory results for those conditions (Ragab 1995), but the model was not used with remotely sensed data as input.

In this paper, remotely sensed θ_{vSL} and in situ measurements are combined in Ragab's model to estimate θ_{vBL} to a depth of 60 cm. First, the original model's ability to reproduce measured time series of θ_{vBL} is evaluated using measured meteorological, soil, and vegetation conditions at 4 experimental sites within the study area and period (18 June–16 July 1997) of the SGP '97 experiment.

Model simulations tend to drift because numerical algorithms are simplifications of complex physical processes. Because of this drift, data assimilation techniques may be employed whereby measured data are incorporated into the model to initialize or constrain the model to produce more realistic simulations. Applications of data assimilation arose within the meteorological community (Daley 1991), but the application of these techniques to remote sensing and soil water modeling is relatively new (e.g., Calvet et al. 1998, Houser et al. 1998, Wigneron et al. 1999a, 1999b; Hoeben and Troch 2000, Walker et al.

2001). A number of data assimilation techniques exist and they vary in complexity (Walker et al. 2001). The direct insertion technique is used herein to determine if assimilation of frequent, regularly-spaced field measurements of θ_{vSL} improves model estimations of θ_{vBL} compared to that provided by the original model. Next, the effect of assimilating field-measured θ_{vSL} at irregular intervals is assessed. Lastly, remotely sensed estimates of θ_{vSL} are assimilated into the model to detect the effects of remotely sensed observations of θ_{vSL} on model estimates of θ_{vBL} .

Materials and Methods

Site Descriptions

Four study sites within the SGP '97 experimental area were chosen for model evaluation. Three of the sites (LW02, LW06, LW11) were located on ARS' Little Washita River Experimental Watershed (LWREW), near Chickasha, Okla. (Lat. 34° 53' Long. 98° 07'), and one (ER01) was located at ARS's Grazinglands Research Laboratory near El Reno, Okla. (Fig. 1). All of these sites were classified as native grassland (SGP 1997) and were dominated by big bluestem (*Andropogon gerardii* Vitman), little bluestem (*Schizachyrium scoparium* (Michx.) Nash), indiangrass (*Sorghastrum nutans* (L.) Nash) and switchgrass (*Panicum virgatum* L.). Despite similari-

Table 1. Leaf area index (LAI) and biomass measurements for the study sites. These data were taken from Hollinger and Daughtry (1999).

Site	LAI	Green Standing Biomass			Brown Standing Biomass			Surface Residue (Litter)		
		Wet	Dry	Water Content	Wet	Dry	Water	Wet	Dry	Water Content
		----(gm ⁻²)----	----(gm ⁻²)----	-(%-)-	----(gm ⁻²)----	----(gm ⁻²)----	-(%-)-	----(gm ⁻²)----	----(gm ⁻²)----	-(%-)-
ER01	4.7	1403	460	67	133	97	26	967	510	47
LW02	2.2	350	161	53	184	158	19	160	141	14
LW06	0.9	112	41	62	22	18	17	18	12	10
LW11	3.6	940	246	73	67	44	43	494	319	35

Table 2. Soil particle fractions and texture of the soil profile and taxonomy of the soils for each site.

Site	Sand	Silt	Clay	Texture	Soil taxonomy
	-----	(%)-----	-----		
ER01 silty,	22	60	18	Silt loam	Pond Creek silt loam (fine-silty, mixed, thermic Pachic Argiustolls)
LW02	26	48	26	Loam	Lucien-Nash complex (loamy, mixed, thermic, shallow Udic Haplustolls)
LW06	73	17	10	Sandy loam Haplustalfs)	Dougherty loamy fine sand (loamy, mixed, thermic, Arenic Haplustalfs)
LW11	54	24	22	Sandy clay loam	Nash loam (coarse-silty, mixed, thermic Udic Haplustolls)

ties in species composition, Hollinger and Daughtry (1999) showed that other vegetation conditions varied widely between sites during the study period. For example, the leaf area index at ER01 was 4.7, while that at LW06 was 0.9. Additionally, litter mass at ER01 measured 510 g m⁻² (on a dry matter basis), which is about 1.5 times that measured at site LW11 and 42 times that at LW06 (Table 1).

The soil profile at each site was sampled to a depth of 60 cm in 15 cm depth intervals using a coring tool with a 5 cm inside diameter. Depth intervals were divided into 7.5 cm long sub-samples. One sub-sample was used to determine soil texture using the hydrometer method (Day 1965). Soil texture for the total soil profile was

calculated as the average of the sand, silt, and clay fractions of the four subsamples (Table 2). The remaining sub-sample was used to determine the soil water release curve at each depth interval using the procedure given in Ahuja et al. (1985). Soil water release curves allow conversion of soil matrix potential (ψ), the measure of the soil matrix capillary and absorptive forces exerted on water, into estimates of θ_v . Laboratory determination of the soil water release curves provided direct measurement of bulk density and the required model parameters of θ_v at saturation (θ_{vS}), field capacity (θ_{vFC}), and wilting point (θ_{vWP}) (Table 3).

Table 3. Surface (0-5cm) and soil profile (0-60cm) volumetric soil water contents (θ_v) at field capacity (FC), wilting point (WP) and saturation (S) used in the model.

Site	Layer	θ_{vFC}	θ_{vWP}	θ_{vS}
		----- m ³ m ⁻³ -----		
ER01	Surface	0.32	0.24	0.41
	Soil profile	0.32	0.24	0.40
LW02	Surface	0.32	0.17	0.38
	Soil profile	0.31	0.11	0.35
LW06	Surface	0.17	0.02	0.44
	Soil profile	0.17	0.02	0.41
LW11	Surface	0.29	0.05	0.38
	Soil profile	0.29	0.06	0.42

Meteorological and θ_v Field Measurements

Air temperature, rainfall, relative humidity, wind speed, incoming solar radiation, and barometric pressure were recorded at meteorological stations located at or near each study site. These data were used in a Penman-Monteith equation to calculate potential ET (ET_p) at sites LW06 and LW11. Actual ET (ET_a) was calculated at sites ER01 and LW02 using the Bowen ratio/energy balance approach (Rosenberg et al. 1983).

A Soil Heat and Water Measurement System (SHAWMS) was installed at each of the 4 sites prior to SGP '97. Each SHAWMS was placed inside a fenced enclosure measuring about 3.7 m on a side and about 1.3 m high. The vegetation within the enclosure was monitored regularly and managed to match surrounding field conditions as closely as possible. The SHAWMS instrumentation includes soil heat dissipation sensors (HDS) (Model 229, Campbell Scientific, Inc., Logan, Utah) which provided hourly measurements of ψ with 3 replications at 5 cm and 1 replication each at 10, 15, 20, 25, and 60 cm below the soil surface. All HDSs were calibrated according to the method outlined in Starks (1999). Conversion of ψ to θ_v was based on the site- and depth-specific soil water release curves. The SHAWMS HDS output at 1200 hours (CST) was used to represent daily θ_v since it was nearly co-incident with the time that the remotely sensed data were obtained over the area. Measured θ_{vBL} was calculated as a weighted average of the HDS readings.

Elliott et al. (1999), Humes et al. (1999), Schneider et al. (1999), and Starks et al. (1999) found good correspondence between θ_v derived from HDSs and gravimetrically-based values, and to values obtained from various types of electronic sensors. The HDS-derived θ_v tended to overestimate gravimetrically obtained values by about 0.02 m³m⁻³, on average, at 3 study sites in Oklahoma (Starks 1999). When a sandy site was eliminated from the analysis, the overestimation was ≤ 0.01 m³m⁻³. Humes (personal communication) compared θ_v derived from both HDS and that determined gravimetrically from soil cores at a number of locations in Oklahoma and found that the HDS values

¹Names are necessary to report factually on available data; however, the USDA neither guarantees or warrants the standard of the product, and the use of the name by the USDA implies no approval of the product to the exclusion of others that may also be suitable.

were within about $0.05 \text{ m}^3\text{m}^{-3}$ of those obtained from the soil cores.

The HDSs tend to lose hydraulic contact with sandy soils and do not yield consistently reliable data under those conditions (Starks 1999). Therefore, at sites LW06 and LW11, gravimetric and time-domain reflectometry (TDR) measurements were used to determine θ_{VSL} and θ_{VBL} , respectively. The TDR measurements at these 2 sites were obtained daily (weather permitting) during the 16 June–18 July experimental period within 2 hours of the remotely sensed data. An Environmental Sensors' MoisturePoint TDR (G.S. Gabel Corporation, British Columbia, Canada), utilizing 4-segment profiling rods, was used to sample the soil profile at 0–15, 15–30, 30–45 and 45–60 cm. Three readings were acquired per site per layer and were averaged to represent daily θ_{VBL} . The manufacturer's stated accuracy of the TDR is $\pm 3\%$ of the instrument reading.

Nine soil samples, representing the 0–5 cm surface layer, were collected once daily over a 20 m by 20 m grid at each site. Gravimetric soil water content was determined for each sample, averaged and multiplied by the respective soil's bulk density to obtain a representative value of θ_{VSL} for each site. Standard deviations of the gravimetric soil water contents ranged between 0.01 and $0.04 \text{ m}^3\text{m}^{-3}$.

Remotely Sensed Data

Remotely sensed images of surface microwave brightness temperatures (T_B) were acquired over the 10,000 km^2 SGP '97 study area using the Electronically Scanned Thinned Array Radiometer (ESTAR). The ESTAR is an L band, synthetic aperture, passive microwave radiometer operating at a center frequency of 1.413 GHz (21 cm) and a bandwidth of 20 MHz. The ESTAR instrument was flown onboard a NASA P3B aircraft at an altitude of 7.5 km. Postprocessing of the remotely sensed data produced a pixel size of 800 m by 800 m. Because of weather conditions and equipment failures, the ESTAR was only able to collect data on 16 days of the 29 day study period. Nominal time over target was 0930 to 1130 hours local time.

Brightness temperatures measured by ESTAR are affected by a number of surface conditions which must be taken into account before a final θ_{VSL} can be determined. Figure 2 is a diagram of the soil moisture retrieval algorithm used to convert T_B to θ_{VSL} . Input requirements for the model are soil temperature at 15 cm, vegetation type, vegetation water content,

soil roughness, and soil texture. The model corrects T_B for vegetation cover and surface roughness, and then estimates the soil's dielectric constant. Soil texture effects are then taken into account before inverting the dielectric mixing model (Wang and Schmugge 1980) to provide the final remote sensing images of θ_{VSL} . For additional details of the soil moisture algorithm see Jackson (1993).

Study site latitude and longitude coordinates were used in an image processing system to locate and extract θ_{VSL} values from the ESTAR images, which were subsequently assimilated into the model.

The Model

The model is a one-dimensional soil water budget algorithm based on the force-restore concept presented by Bhumralkar (1975) for soil temperature, later adapted to soil water movement by Deardorff (1977). The model is divided into a surface layer (the remote sensing depth, 0–5 cm for this study) and a layer that extends from the soil surface to a user-defined depth (termed bulk layer by Ragab). In the remainder of this paper the term bulk layer will be used in preference to soil profile.

The model operates on a daily time step and the required meteorological data are daily values of rainfall and ET_p . The ET_p values are adjusted within the model by a stress factor to estimate ET_a . The stress factor is the ratio of actual available to maximum available soil water content. The model was modified to bypass the stress adjustment when measured ET_a values are used. Required soil parameters include depth of the surface and bulk layers; and, for each layer, θ_{VFC} (θ_v corresponding to ψ of -33 kPa), θ_{VWP} (θ_v corresponding to ψ of -1500 kPa), antecedent θ_v (initial soil water content at the beginning of the model run), and maximum and minimum model-allowed θ_v (prevents model estimates from being unrealistically wet or dry). The user can partition a portion of incident rainfall into runoff through the "surface runoff percentage" variable. This variable is initialized at the beginning of the model run and all subsequent rainfall events are partitioned in the same fashion. Since most rainfall events that occurred in this study were light, this variable was set to zero (i.e., no runoff). The "uptake ratio" variable is used to define the surface layer's contribution to ET_a . In this study the uptake ratio was set to 0.25 at all sites.

Dynamically, θ_{VSL} is determined as a function of rainfall, runoff, ET_a , and the

Fig. 2. Schematic of the soil moisture retrieval algorithm (adapted from Jackson, 1993).

amount of water in the bulk layer. The rate of exchange of water between the surface and bulk layer is governed by a pseudo-diffusivity coefficient (C), which depends upon surface soil texture and θ_{VBL} . The value of C at our four study sites was empirically determined by running the model at sites with similar soils and making adjustments to C until the best match between model output and measured data was achieved.

Calculation of θ_{VBL} is independent of surface layer computations and is a simple water budget requiring only daily values of rainfall, runoff, and ET . Thus, assimilation of surface θ_{VSL} measurements into the original model will not affect bulk layer calculations. Therefore the original model was re-written in order that measurements of θ_{VSL} could be assimilated into the model to infer θ_{VBL} . To this end, we adapted the statistical procedure outlined in Ragab (1995) for determining model initialization values for the bulk layer from surface measurements. This procedure utilizes site-specific linear regression equations, developed from field

Table 4. Slope, intercept and coefficient of determination (r^2) of linear regression equations used to convert remotely sensed surface θ_v to root zone soil water storage (mm). Root zone soil water storage is divided by depth of the root zone to estimate root zone θ_v .

Site	slope	intercept	r^2
ER01	387.76	67.13	0.60
LW02	309.58	67.02	0.74
LW06	409.96	43.21	0.96
LW11	307.96	86.33	0.90

measurements, which relate θ_{vSL} (in m^3m^{-3}) to the depth of water stored (in mm) in the bulk layer. Soil water storage values from the regression equations are divided by the bulk layer depth to yield updated values of θ_{vBL} . Correlation coefficients from the linear regressions (Table 4) are similar to those reported by Ragab (1995) for 2 soils in southern England.

The model was run for 4 scenarios. The first scenario examines the original model's ability to simulate θ_{vBL} for the meteorologic, soil, and vegetation conditions at each of the study sites. In this scenario the initial θ_{vBL} values are supplied from field-measured data. The model then produces a time series of θ_{vBL} based only upon the meteorological drivers of rainfall and ET_a and the measured soil and vegeta-

tion parameters initially supplied to the model. In the second scenario, field measurements of θ_{vSL} are assimilated into the model at 2-day intervals to determine if model simulations of θ_{vBL} are improved over that of scenario 1. The 2-day interval was chosen in response to the frequency of surface soil moisture products that may become available on future satellite platforms. For example, the European Space Agency's ENVISAT has a primary repeat coverage cycle of 35 days, but will have coverage subcycles of 1, 3, and 17 days (<http://envisat.esa.int/> accessed 7 Jan. 2002). In scenario 3, field measurements are again used to update the model but only on those days corresponding to the times when the ESTAR was used to collect data during the study period. Since the ESTAR did not fly every day during the study period, this scenario examines the effect of irregular and/or infrequent data assimilation on model simulations during the study period. In the fourth scenario, ESTAR data, which represents a 800 m by 800 m spatial average of θ_{vSL} , are assimilated into the model.

Statistical Analysis

Willmott and Wicks (1980) and Willmott (1981, 1982) raised concerns

about the exclusive use of r and r^2 in the context of evaluating model performance. Willmott (1981) noted that very dissimilar values of measurements and estimates can produce an r very near 1, while small differences between measured and estimated quantities can produce a low or even negative r (Willmott and Wicks 1980). Willmott (1982) proposed the d-index of model agreement which, when used in conjunction with other common statistical measures, aids in evaluating the accuracy of models. A $d = 1$ indicates complete agreement between modeled and measured values, and $d = 0$ indicates complete disagreement. The d-index is used herein to evaluate how well model output agrees with measured field data for each of the 4 scenarios. In addition, the mean error (ME) and root mean square error (RMSE) were used to describe the average difference between modeled and measured values and to describe the average total error in the estimating procedure, respectively. A no-intercept linear regression analysis was used to determine r^2 and regression coefficients (slope, designated β_1) between measured and modeled values. A t -test was used to determine if the modeled values are significantly different from measured values by testing the null hypothesis, $H_0: \beta_1 = 1$. Preliminary analy-

Fig. 3. Time series plots of measured and modeled bulk layer volumetric soil water content for study sites ER01 (a), LW02 (b), LW06 (c), and LW11 (d) during the experimental period. Gaps in the time series reflect days when measured values were unavailable for comparison with modeled output.

Table 5. Results from the statistical analysis of the comparison of modeled and measured bulk layer soil water content for each scenario.

Site ID	Scenario 1					Scenario 2				
	d ¹	ME ²	RMSE	β_1	r ²	d	ME	RMSE	β_1	r ²
		-----(m^3m^{-3})-----					-----(m^3m^{-3})-----			
ER01	0.25	0.05	0.06	1.201**	0.990	0.58	0.01	0.01	1.028	0.999
LW02	0.52	0.02	0.03	1.088**	0.996	0.59	0.01	0.01	1.018	0.997
LW06	0.56	0.04	0.05	1.399**	0.985	0.78	0.00	0.02	1.000	0.972
LW11	0.69	0.05	0.06	1.235**	0.973	0.88	0.01	0.03	1.014	0.984

Site ID	Scenario 1					Scenario 2				
	d ¹	ME ²	RMSE	β_1	r ²	d	ME	RMSE	β_1	r ²
		-----(m^3m^{-3})-----					-----(m^3m^{-3})-----			
ER01	0.37	0.01	0.02	1.021	0.995	0.23	0.04	0.05	1.142**	0.989
LW02	0.66	0.01	0.02	1.037	0.997	0.12	0.15	0.15	2.371**	0.982
LW06	0.72	0.01	0.03	0.984	0.956	0.73	0.02	0.03	1.123**	0.986
LW11	0.97	0.00	0.02	0.995	0.998	0.91	0.00	0.02	0.984	0.991

**Significant at the 0.01 level

¹d = $1 - [\sum(\text{Modeled} - \text{Measured})^2 / \sum(\text{Modeled} - \text{Mean of Measured})^2 + \sum(\text{Measured} - \text{Mean of Measured})^2]$

²ME = $\sum(\text{Measured} - \text{Modeled}) / n$

³RMSE = $[\sum(\text{Modeled} - \text{Measured})^2 / n]^{1/2}$

sis showed that the residual lack of fit in the no-intercept regression analyses was small and not a realistic estimate of the true error because of the extremely good fit of the model output to the measured data. Thus, an error of $0.03 \text{ m}^3\text{m}^{-3}$ in the HDS and TDR measurements is assumed and is used as an approximation of the standard error of the estimate in the t -equation. Since the study objective relates to the bulk layer, only the results from that layer are reported.

Results

Scenario 1 - Original Model

The range of measured θ_{vBL} over the course of the study period was about $0.04 \text{ m}^3\text{m}^{-3}$ at sites ER01 and LW02, $0.08 \text{ m}^3\text{m}^{-3}$ at LW06, and $0.14 \text{ m}^3\text{m}^{-3}$ at LW11. These ranges of measured θ_{vBL} represent 50, 20, 93, and 61% of the total plant available water (defined as the difference in water content at field capacity and wilting point) at these sites, respectively. Time series simulations from the original model exhibit the general patterns portrayed by the measured data, but the model consistently underestimated measured values at all sites (Figs. 3a–3d). The differences between measured and modeled θ_{vBL} generally increase with time at sites ER01 and LW02, while at sites LW06 and LW11 there appears to be a constant offset or bias in the model simulations (Figs. 3a–3d).

The r^2 values indicate that the variation in the modeled values is strongly associated with the variation in the measurements at all sites (Table 5), but the β_1 are significantly different from a slope of 1, indicating that the modeled output does not

approximate measured values well. The d-index (Table 5), however, indicates weak agreement between measured and modeled values at ER01, moderate agreement at sites LW02 and LW06, and stronger agreement at LW11. The ME reveals that the model underestimated measured values from $0.02 \text{ m}^3\text{m}^{-3}$ at site LW02 to $0.05 \text{ m}^3\text{m}^{-3}$ at site ER01. Only site LW02 had a $\text{RMSE} \leq 0.05 \text{ m}^3\text{m}^{-3}$.

Scenario 2

Assimilation of field-measured θ_{vSL} values into the model at frequent, evenly-spaced intervals brings the model estimates of θ_{vBL} into close agreement with measured values (Figs. 3a–3d). Neither the steadily increasing differences or constant offset from measured values noted in the simulations of scenario 1 is observed here.

The d-index increased at all sites, with the greatest improvement observed at ER01. At all study sites, the RMSE were $\leq 0.03 \text{ m}^3\text{m}^{-3}$, a two-fold reduction at each site compared to scenario 1 (Table 5). The absolute values of ME were all $\leq 0.01 \text{ m}^3\text{m}^{-3}$, a reduction of at least $0.04 \text{ m}^3\text{m}^{-3}$ at all sites, except at LW02 where the ME was reduced by $0.01 \text{ m}^3\text{m}^{-3}$. The β_1 values at all sites were not significantly different from a slope of 1, indicating that the model output closely approximates the measured values.

Scenario 3

Assimilation of field-measured θ_{vSL} into the model at irregular intervals produced mixed results. At site ER01, the d-index decreased considerably in comparison to scenario 2, although the ME remained unchanged and the RMSE increased by only $0.01 \text{ m}^3\text{m}^{-3}$ to $0.02 \text{ m}^3\text{m}^{-3}$ (Table 5). Comparison of the time series plots (Fig.

3a) shows that scenarios 2 and 3 produced similar output except during consecutive days when assimilation data were unavailable (DOY 172–175, 185–191). At site LW02, the d-index increased slightly over that observed in scenario 2, the ME remained unchanged and the RMSE increased by $0.01 \text{ m}^3\text{m}^{-3}$. The largest discrepancies between measured and modeled data at site LW02 occurred during the 7 days from DOY 185–191 (Fig. 3b) when field measurements of θ_{vSL} were not available to the model. The effect of assimilating θ_{vSL} data at irregular intervals had a small negative effect at site LW06 (Fig. 3c) as indicated by a slight decrease in the d-index and an increase of $0.01 \text{ m}^3\text{m}^{-3}$ in the ME and RMSE (Table 5) over that observed in scenario 2. At site LW11 (Fig. 3d) the d-index (Table 5) indicates near-perfect agreement between modeled and measured values. Additionally, the ME and RMSE decreased by $0.01 \text{ m}^3\text{m}^{-3}$ from those observed in scenario 2. It should be noted that the statistical analysis from this scenario shows improved simulations at all sites over that obtained in scenario 1; all d-indices are larger and all ME and RMSE values smaller than their counterparts in scenario 1. As in scenario 2, the β_1 values were found to be statistically similar to a slope of 1.

Scenario 4

Model output at sites ER01 and LW02 did not agree well with measured data (d-index ≤ 0.23) (Figures 3a–d, Table 5). At site ER01, both the ME and RMSE increased by $0.03 \text{ m}^3\text{m}^{-3}$ over that observed in scenario 3. Regression coefficients at these 2 sites are statistically different from a slope of 1, suggesting that

modeled θ_{vBL} does not adequately approximate measured values. At site LW02, assimilation of remotely sensed θ_{vSL} into the model produced ME and RMSE values larger than any others encountered in the study. In contrast, the d-index, ME and RMSE values at sites LW06 and LW11 are comparable to those in scenarios 2 and 3, indicating good agreement with measured values. However, the β_1 at LW06 is statistically different from a slope of 1.

Summary and Conclusions

The objective of this paper was to examine the feasibility of inferring θ_{vBL} by combining remotely sensed estimates of surface water content, in situ measurements, and modeling techniques. The model of Ragab (1995) was selected for this study because of its simplicity and because it does not require detailed soil physical and hydraulic and vegetation properties to parameterize the model—properties that are not generally available or easily measured over large and/or spatially variable watersheds. This is particularly advantageous for applications where little is known about an area's soil physical properties, since the required model inputs may be estimated from general soil texture information (e.g., Rawls et al. 1982).

The original model was able to reproduce the time series patterns of θ_{vBL} , but consistently underestimated measured values from 0.02 to 0.05 m^3m^{-3} , on average, depending upon study site. Underestimation of θ_{vBL} may be a result of overestimation of daily ET_a . The simplistic stress factor adjustment used in the model, to reduce the user-supplied daily ET_p values to more closely approximate ET_a , is calculated as the ratio of actual water available in a given layer of the soil to the maximum amount of water that layer could hold. This adjustment algorithm does not explicitly take into account the various resistances that may reduce the flow of water from the soil, through the plant and into the atmosphere. At 2 study sites, measured values of ET_a were used in place of ET_p , and the stress factor adjustment bypassed in the model. Even at these sites, ET_a may have been overestimated since the values supplied from the Bowen ratio measurements may have reflected contributions from below the 0–60 cm layer that was modeled.

Since numerical algorithms are approximations of complex physical processes, the model was re-written to determine if

assimilation of θ_{vSL} observations could improve model estimates of θ_{vBL} . The data assimilation technique used either field-measured or remotely sensed θ_{vSL} values in site-specific linear regression equations to infer θ_{vSL} within the model. When field observations of θ_{vSL} were assimilated at regular and frequent intervals (scenario 2), the model simulations were improved and model output agreed well with measurements at all sites. When the field observations were assimilated at irregular intervals (scenario 3), model output agreed well with measured data at all but 1 site. However, scenario 3 simulations at all study sites showed improvement over that provided by the original model (scenario 1). In general, assimilation of field-measured θ_{vSL} into the model resulted in θ_{vSL} estimates that compared well to measured values.

Remotely sensed observations of θ_{vSL} were assimilated into the model to determine the effects on estimation of θ_{vBL} (scenario 4). Modeling results at sites LW06 and LW11 were similar to those produced by scenarios 2 and 3 (i.e., good agreement between measured and modeled values as indicated by the d-index, ME and RMSE statistics). Results from the *t*-tests showed that the β_1 obtained at LW06 was statistically different from a slope of 1, suggesting that the modeled output did not agree well with the measured data. The reason for this is not clear since the statistics (d-index, ME and RMSE) from scenario 4 are very similar to those from scenario 3 at this site. It is not likely that the vegetation adversely affected the remotely sensed data (discussed below) because LW06 had the lowest leaf area index of all the study sites. It is possible that the measured θ_{vBL} data (obtained at a point) did not adequately represent the 800 x 800 m area observed by the remotely sensed data.

When remotely sensed data were assimilated into the model at sites ER01 and LW02, the model output underestimated measurements throughout the study period. At site ER01, the modeling results were similar to those observed in scenario 1, but the simulation at site LW02 underestimated measured values by about 0.15 m^3m^{-3} throughout the study period. Underestimation of θ_{vBL} at these 2 sites is apparently a result of vegetational effects on the ESTAR data. Jackson et al. (1999) noted that tall grasses and heavy litter deposits will cause the ESTAR moisture retrieval algorithm to underestimate θ_{vSL} . Site ER01 was the most densely vegetated of the study sites and possessed the heaviest

litter layer. Although site LW02 was classified as a rangeland site, there are a number of trees in the area and, like tall grasses and dense litter layers, trees lead to underestimation of ESTAR θ_{vSL} . Thus, assimilated remotely sensed θ_{vBL} values from these sites probably led to underestimated bulk layer values. Jackson et al. (1999) indicated that adjustments to vegetational aspects of the ESTAR soil moisture retrieval algorithm can be made to better account for litter and trees. These adjustments will be necessary if microwave-based remote sensing techniques are to be widely used to assess soil water content. The results from scenario 4 suggest that it is feasible to infer θ_{vBL} in tallgrass prairies by combining remotely sensed observations of θ_{vBL} into a soil water budget model, provided that the remotely sensed data has not been corrupted by vegetational effects.

The assimilation procedure used in this study was based upon a linear regression approach suggested by Ragab (1995) for determining bulk layer model initialization values from surface measurements. This approach is simple, and worked well at the study sites over the course of the study period, but the approach is empirical and may not produce satisfactory results over longer periods or in the presence of layered soils (e.g., sandy textured surface soil overlaying clay). An alternate approach would be to use a multiple regression equation that would take into account time since the last rainfall event, precipitation amount, and soil texture. The linear equations developed here should not be expected to apply to other locations having different soil, vegetation, and climate conditions.

A remote sensing/modeling approach such as that described above could be integrated with weather forecasts and/or climate outlooks to project future soil water supplies, as well as assessing the current status of soil water content. Such assessments and predictions could be used by agricultural producers and others to schedule irrigation and predict crop or forage production rates, and by water resources managers to better manage watersheds and surface, soil, and groundwater water resources.

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Quality and persistence of forages in the Northern Great Plains

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Abstract

Integrating use of seedings of perennial cool-season grasses with native range is used to increase available forage and for maintaining a high plane of nutrition for grazing livestock. Our goal was to evaluate performance of yearling cattle and stand persistence of 3 released wheatgrass cultivars. Twice replicated 3-ha pastures were seeded to 'Rosana' western wheatgrass [*Pascopyron smithii* (Rydb.) A. Love], 'Luna' pubescent wheatgrass [*Elytrigia intermedia* (Host) Nevski], and 'Hycrest' crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.] ssp. *desertorum* (Fisch. ex Link) A. Love in autumn 1994. Yearling steers ($n = 8$) grazed from 9 May to 12 June 1997 and 24 April to 15 June 1998. Yearling heifers grazed from 27 April to 18 June 1999. Hycrest produced the largest herbage standing crop in spring 1997 (912 kg ha⁻¹) and 1998 (1,223 kg ha⁻¹) ($P < 0.05$), but by spring 1999 standing crops averaged 656 kg ha⁻¹, and cultivars were not significantly different. Digestible organic matter standing crop did not differ among pastures of seeded species, but declined ($P < 0.05$) from May to June each year. Crude protein standing crop varied among cultivars ($P < 0.05$) in April and May 1998 and May 1999; however, no clear trends emerged. Crude protein standing crops consistently declined from April-May to June. Average daily gains were similar among cultivars in 1997, but greater ($P < 0.05$) on Hycrest (1.28 kg day⁻¹) than Rosana (1.03 kg day⁻¹) in 1998. Gains on Hycrest (0.74 kg day⁻¹) and Rosana (0.78 kg day⁻¹) were greater ($P < 0.05$) than on Luna (0.52 kg day⁻¹) in 1999. These findings show in some years, Hycrest provided more forage in spring than Rosana, and will allow an increase in livestock numbers. Based on the encroachment of invading species, persistence of Luna is marginal of the 335-mm precipitation zone in the Northern Great Plains.

Key Words: *Agropyron* spp. *Pascopyron smithii*, *Elytrigia intermedia*, Hycrest, Luna, Rosana, crude protein, digestibility, standing crop

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Resumen

La integración de siembras de zacates perennes de estación fría con el pastizal nativo es usado para incrementar la disponibilidad de forraje y para mantener un plano nutricional alto del ganado en apacentamiento. Nuestra meta fue evaluar el comportamiento de novillos y vaquillas y la persistencia de la poblaciones de 3 cultivares liberados de "Wheatgrass". En otoño de 1994, en potreros de 3 ha repetidos 2 veces, se sembraron "Western wheatgrass" [*Pascopyron smithii* (Rydb.) A. Love] variedad 'Rosana', "Pubescent wheatgrass" [*Elytrigia intermedia* (Host) Nevski] variedad 'Luna' y "Crested wheatgrass" [*Agropyron cristatum* (L.) Gaertn.] ssp. *desertorum* (Fisch. ex Link) A. Love} variedad 'Hycrest'. Los novillo ($n = 8$) apacentaron del 9 de mayo al 12 de junio de 1997 y del 24 de abril al 15 de junio de 1998. Las vaquillas apacentaron del 27 de abril al 18 de junio de 1999. La variedad 'Hycrest' produjo la mayor cantidad de biomasa en pie en 1997 (912 kg ha⁻¹) y en 1998 (1,223 kg ha⁻¹) ($P < 0.05$), pero para la primavera de 1999 la biomasa en pie promedió 656 kg ha⁻¹ y no hubo diferencia significativa entre cultivares. La MO digestible de la biomasa en pie no difirió entre las especies sembradas, pero disminuyó ($P < 0.05$) de mayo a junio de cada año. La proteína cruda del forraje en pie varió entre cultivares ($P < 0.05$) en abril y mayo de 1998 y en mayo de 1999; sin embargo, no se definieron tendencias claras. La proteína cruda disminuyó consistentemente de abril-mayo a junio. En 1997, las ganancias diarias promedio fueron similares entre cultivares, pero en 1998 fueron mayores ($P < 0.05$) para 'Hycrest' (1.28 kg day⁻¹) que para 'Rosana' (1.03 kg day⁻¹). En 1999, las ganancias en 'Hycrest' (0.74 kg day⁻¹) y 'Rosana' (0.78 kg day⁻¹) fueron mayores ($P < 0.05$) que las obtenidas con 'Luna' (0.52 kg day⁻¹). Estos hallazgos muestran que en algunos años 'Hycrest' provee más forraje en primavera que 'Rosana', lo que permitirá un aumento en el número de ganado. Basado en la dispersión de especies invasoras la persistencia de 'Luna' es marginal en la zona de precipitación de 335 mm de las Grandes Planicies del Norte.

Pastures seeded to perennial cool-season grasses can be used to reduce grazing pressure on native ranges and provide quality forage for livestock at selected seasons (Wight et al. 1983). Many seeded grass species, cultivars, and hybrids have been evaluated for forage production and nutrient quality and persistence on selected sites, then subsequently recommended for use over a wide area (Vallentine 1980, Currie and White 1982, Currie et al. 1986b). Although some have been evaluated for livestock preference (Truscott and Currie 1989, Borman et al. 1991), few have

been evaluated for livestock performance before release (Smoliak 1968, Smoliak and Slen 1974, Kilcher and Lawrence 1979, Hart et al. 1983, Hofmann et al. 1993). Also, studies by Moore et al. (1995) and Vogel et al. (1993) clearly show that grazing studies provide additional information on livestock rate of gain and stand persistence that cannot be obtained with small plot evaluations. For example, Papadopoulos et al. (1995) compared orchardgrass (*Dactylis glomerata* L.) cultivars in haying and grazing systems and found the cultivars ranked differently between the 2 systems. Thus, it appears that grazing trials are needed to compare experimental cultivars. The goal of this project was to evaluate livestock performance and stand persistence of introduced and native cultivars of 3 released wheatgrasses.

Materials and Methods

Study Site

Research was conducted at the Fort Keogh Livestock and Range Research Laboratory (46°22'N 105°5'W) near Miles City, Mont. Elevation on the study site is 719 m. Regional topography varies from rolling hills to broken badlands with small intersecting ephemeral streams flowing into rivers in broad, nearly level valleys. This area is representative of the semi-arid mixed grass prairie of the Northern Great Plains. Indigenous vegetation on the

22,500-ha research station is a grama-needlegrass-wheatgrass (*Bouteloua-Stipa-Agropyron*) mix (Küchler 1964). Annual precipitation averages 343 mm, with about 60% received from April through September (Fig. 1). Daily temperatures range from > 38°C during summer to < -40°C during winter. The average frost-free growing season is 150 days. Soils on the site are a composite of Glendive loam (coarse-loamy, mixed, superactive, calcareous, frigid Aridic Ustifluvents) and Havre loam (fine-loamy, mixed, superactive, calcareous, frigid Aridic Ustifluvents) with 0 to 2% slopes.

Treatments and Experimental Design

Six, 3-ha pastures, previously seeded to crested wheatgrass [*Agropyron cristatum* (L.)] or Russian wildrye [*Psathyrostachys juncea* (Fisch.) Nevski], combined with alfalfa (*Medicago sativa* L.) were used in this study. Seedbeds were prepared by spraying vegetation with Roundup [Glyphosate, N-(phosphonomethyl) glycine] in early summer 1994, disking in late summer, and then rototilling and seeding with the Range Improvement Machine (RIM) (Currie et al. 1986a) during late autumn. Each forage species was planted in 2 of 6 pastures arranged in randomized-complete-block design with 2 blocks of 3 treatment species in autumn 1994. Forages were 'Rosana' western wheatgrass [*Pascopyron smithii* (Rydb.) A. Love], 'Luna' pubescent wheatgrass [*Elytrigia*

intermedia (Host) Nevski], and 'Hycrest' crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.] ssp. *desertorum* (Fisch. ex Link) A. Love}. Seeds were drilled in rows on 30-cm centers with the RIM machine (Currie et al. 1986a). Seedlings were hayed but not grazed during 1995 and 1996. Stubble resulting from growth after grazing during 1997, 1998, and 1999 was left standing.

Each 3-ha pasture was stocked with 8 crossbred yearling steers of British breed origin (*Bos taurus*) from 9 May to 12 June 1997 and 24 April to 15 June 1998. Due to lack of availability of steers, each pasture was stocked with purebred yearling Hereford heifers from 27 April to 18 June 1999. Livestock were handled according to protocol approved by the Fort Keogh Livestock and Range Research Animal Care Committee. Availability of herbage in the least productive pasture (block 1 Luna) determined the time of livestock removal.

Field Measurements

At the beginning of each grazing season animals were weighed, stratified by initial weight, and within strata randomly assigned to pastures. Thereafter, weights were obtained at the start and then about every 30 days, and at the end of each annual trial. Initial weights of animals averaged 348 kg (SD = 29) in 1997, 363 kg (SD = 20) in 1998, and 363 kg (SD = 20) in 1999. Animals were treated with Ivermectin¹ (Merck & Co. Inc., Whitehouse Station, N.J.) before the study for parasite control and received an ear tag with fly repellent at the beginning of the grazing season. Trace mineralized salt was available at all times.

Standing crop was sampled during the weeks livestock were weighed by clipping forage to ground level in fifteen, 0.25 m² quadrats in each 3-ha pasture. Forage samples were oven dried in a forced draft oven at 60°C and weighed. May 1997 and April 1998 and 1999 samples were separated into the following 4 portions: green tissue of seeded species, other grasses, and forbs and standing dead herbage. Samples collected during June 1997 and May and June 1998 and 1999, the middle and end of the grazing period, were separated by seeded species (live + dead or senesced tissue) and other species (live + dead or senesced tissue). Dead biomass simply reflects the combination of forage remaining after the grazing season plus that which was produced after cattle were removed. Relatively large amounts (1,000 kg ha⁻¹) of dead may remain standing over winter when snow cover is light.

Fig. 1. Precipitation recorded on the Houston pasture study site (shaded bars) at Fort Keogh and at the Frank Wiley Airfield located about 4 km from the study site (open bars) and long-term average from Frank Wiley Airfield (National Oceanic and Atmospheric Administration 1994-1999).

Diets were sampled monthly for each seeded grass during the week animals were weighed in 1998 and 1999. Six to 8 esophageally cannulated crossbred cows were used for diet sample collection. Diets were collected from 2 cows per pasture in 1998 and 3 cows per pasture in 1999, but not all pastures were sampled with the same cows. Cows were penned at 1600 hours with water but no feed available. Collections were made the following morning beginning at 0700 hours. Collection periods lasted from 20 to 30 min. and were followed immediately by a collection in a second pasture. Esophageal masticate samples were thoroughly mixed by hand, and freeze dried for diet quality analyses. These cows were about 3 to 5 years old when sample collections began. Cows had been cannulated at 2 months of age and were experienced with the diet collection process. Between sampling periods, cows were kept in larger pastures with a variety of range sites but not the grass cultivars being assessed. However, cows had been previously exposed to all plant species present in the experimental pastures.

Laboratory Analysis

Two (1998) or 3 (1999) esophageal masticate samples per pasture and 3 standing crop samples of each vegetation component per pasture were ground to pass through a 1-mm screen in a Wiley mill¹ (Arthur H. Thomas Co., Philadelphia, Penn.). Total nitrogen (N) (organic matter basis) was determined on a C-N analyzer (Carlo-Erba¹, C.E. Elantech, Inc., Lakewood, N.J.). Data are presented as CP standing crop (%N * 0.0625 * kg standing crop) and percentage CP in diets. In vitro digestible organic matter (IVDOM) was determined using a modified Tilley and Terry (1963) technique (White et al. 1981). Data are presented as digestible organic matter (OM) standing crop and percentage IVDOM in diets. Crude protein and IVDOM standing crop were summations of all live and dead vegetation components.

Data Summarization and Analysis

Analysis of variance was used to test effects of treatments (seeded species), dates, and interaction between them on standing crop, forage quality, diet quality, and livestock gains. Treatment effects were tested using variation among pastures within treatment as the error term. Effects of date and interaction of date with treatment were tested with residual variation after accounting for all other effects in

Table 1. Means for spring standing crops¹ (significant seeded species by date interaction); standard errors equal ± 82.1 for seeded species, ± 35.8 for forbs, and ± 110.6 for standing dead.

Groups/Years	Hycrest	Luna	Rosana
	----- (kg ha ⁻¹) -----		
Seeded species			
1997-May	912 ^{Ab2}	448 ^{Bb}	608 ^{Ba}
1998-April	1,223 ^{Aa}	680 ^{Ba}	750 ^{Ba}
1999-April	617 ^{Ac}	594 ^{Aab}	723 ^{Aa}
Forbs			
1997-May	143 ^{Ab}	136 ^{Aa}	183 ^{Aa}
1998-April	17 ^{Ac}	82 ^{Aa}	6 ^{Aa}
1999-April	261 ^{Aa}	119 ^{Ba}	96 ^{Ba}
Standing dead			
1997-May	666 ^{Ab}	530 ^{Ab}	644 ^{Ab}
1998-April	1,039 ^{Ba}	886 ^{Ba}	1,548 ^{Aa}
1999-April	901 ^{Aab}	886 ^{Aa}	428 ^{Bb}

¹Samples collected in May 1997 and April 1998 and 1999, the beginning of the grazing period, were separated into the following 4 portions: green tissue of seeded species, other grasses, and forbs and standing dead.

²Within a plant group and date, species means with the same uppercase superscripts are not different ($P < 0.05$). Within a plant group and species, means of dates with the same lowercase superscripts are not different ($P < 0.05$).

the model. The Least Significant Difference (LSD) method ($P \leq 0.05$) protected by a prior F-test ($P \leq 0.05$) was used for comparing treatment means. All differences discussed are significant at the $P \leq 0.05$ level unless otherwise noted.

Results

Impact of Environment

Productive stands were established for each species following the dormant seeding in late autumn 1994. The excellent establishment of seeded stands was partially facilitated by greater than or near average amounts of precipitation in March through July 1995 (Fig. 1). In contrast, precipitation was less than the long-term average in April through June and August through October 1996. This lack of precipitation resulted in a partial die off of Luna stands, particularly on elevated portions of

the pastures. We planned to begin grazing pastures in April 1997, but less than average precipitation from February through June 1997 slowed plant growth on seeded pastures. Thus, the 1997 trial was limited to the period from 9 May to 12 June. Greater than average precipitation during March 1998 and April 1999 maintained good plant growth and allowed grazing from April to June during each of these years.

Growth and Persistence of Grasses

Persistence of seeded stands was partially evaluated by comparing the amount of green biomass of seeded species in the spring standing crop. Hycrest produced the largest standing crop in spring 1997 and 1998. However, by spring 1999 standing crops were similar among all 3 seeded grasses (Table 1). Forbs were most productive on the Hycrest pastures in 1999. This finding combined with the decrease

Table 2. Means for early spring and summer standing crops¹ (significant seeded species by date interaction); standard errors equal ± 190.0 for seeded species and ± 86.5 for other species.

Groups/Years	Hycrest	Luna	Rosana
	----- (kg ha ⁻¹) -----		
Seeded			
June 1997	533 ^{Ad2}	330 ^{Ac}	469 ^{Ad}
May 1998	2,543 ^{Aa}	2,367 ^{Aa}	1,800 ^{Ba}
June 1998	1,643 ^{Ab}	1,032 ^{Bb}	889 ^{Bcd}
May 1999	1,294 ^{ABbc}	890 ^{Bb}	1,470 ^{Aab}
June 1999	901 ^{Ac}	701 ^{Abc}	1,015 ^{Abc}
Other species			
June 1997	13 ^{Ab}	44 ^{Ac}	5 ^{Ab}
May 1998	27 ^{Ab}	153 ^{Abc}	29 ^{Ab}
June 1998	103 ^{ABb}	341 ^{Ab}	73 ^{Bab}
May 1999	398 ^{Ba}	1,055 ^{Aa}	298 ^{Ba}
June 1999	346 ^{Ba}	966 ^{Aa}	234 ^{Bab}

¹Samples collected during June 1997 and May and June 1998 and 1999, the middle and end of the grazing period, were separated by seeded species (live plus dead or senesced tissue) and other species (live plus dead or senesced tissue).

²Within a plant group and date, species means with the same uppercase superscripts are not different ($P < 0.05$). Within a plant group and species, means of dates with the same lowercase superscripts are not different ($P < 0.05$).

Table 3. Means for IVDOM standing crops (date main effects); standard error equals ± 75.5 .

1997		1998			1999		
May	June	April	May	June	April	May	June
----- (kg ha ⁻¹) -----							
889 ^{bc1}	309 ^d	1,307 ^a	1,445 ^a	723 ^c	968 ^b	1,240 ^a	846 ^{bc}

¹Means of dates with same lowercase superscripts are not different ($P < 0.05$).

in standing crop of Hycrest in 1999 suggested the Hycrest stand may have thinned. Standing crop of Luna and Rosana were almost similar among years. Dead biomass, which simply reflects the combination of forage remaining after the grazing season plus that which was produced after cattle were removed, averaged over 1,000 kg ha⁻¹ in 1998 in both the Hycrest and Rosana pastures. This large amount resulted from greater than average precipitation in July and October 1997 (Fig. 1). Neither species nor year significantly affected the amount of other grasses growing in each pasture ($\bar{x}$ = 36 kg ha⁻¹ SD = 104).

Standing crops of all 3 seeded species had declined during the grazing period to near 500 kg ha⁻¹ in June 1997 and 872 kg ha⁻¹ in June 1999, but standing crops were similar among species for these 2 periods (Table 2). In contrast, over 1,500 kg ha⁻¹ of Hycrest remained in June 1998, which was significantly greater than the 1,000 kg ha⁻¹ remaining on Luna and 900 kg ha⁻¹ remaining on Rosana pastures. Standing crop of other plant species was less than 350 kg ha⁻¹ through June 1998 for all species. However, a trend of increasing amounts of other species began for all 3 treatment species, but especially for Luna pastures in June 1997, continued through 1998, and was significant in 1999.

Forage Quality

Digestible organic matter (OM) standing crop did not differ among seeded species (data not shown), but declined ($P \leq 0.05$) during the grazing period from May to June each year (Table 3). The numerical increase in digestible OM standing crop from April to May was not significant in 1998 but was significant in 1999. In vitro digestible OM concentration of green seeded grass herbage was >80% in April while concentrations of green plus dead or senesced seeded grass herbage were >60% in May and >50% in June.

Crude protein (CP) standing crop varied among seeded species ($P \leq 0.05$) in April and May 1998 and May 1999 (Table 4). However, no clear trends were detected among seeded species. Crude protein standing crop consistently decreased from April–May to June. The only exception

was the nonsignificant decline from May to June for Hycrest in 1999. Crude protein concentration of green seeded grass herbage was >17% in April and May (1997) while concentrations of green plus dead or senesced seeded grass herbage were >11% in May and >9% in June. The species by date interaction was significant for CP of seeded grasses. Crude protein of seeded grasses differed on 4 out of 8 dates. No clear trends were detected among seeded species in April and May 1998. However, CP of green plus dead herbage for Luna (13.4 $\pm$ 0.01%) was greater than in Hycrest and Rosana ($\bar{x}$ = 9.8 $\pm$ 0.01%) in June 1999 and Hycrest (14.8 $\pm$ 0.01% vs 11.6 $\pm$ 0.01%) in May 1999.

The species by date interaction was also significant for CP of other grasses. A difference occurred among the seeded cultivars on 1 date, June 1999, when other grasses growing on Hycrest plots contained greater concentrations of CP (16.9 $\pm$ 0.01%) than grasses growing on the Luna and Rosana pastures ($\bar{x}$ = 10.5 $\pm$ 0.01%). Crude protein of standing dead varied significantly only among dates and not among seeded species. Crude protein

of standing dead was greatest in April 1999 (8.6 $\pm$ 0.004%), intermediate in April 1998 (7.1 $\pm$ 0.004%), and least in May 1997 (4.7 $\pm$ 0.004%). No significant differences were found for CP in forbs (24.0% SD = 0.04).

Diet Quality

Digestibility of diets declined from April to June in all pastures in 1998 and 1999 (Table 5), but digestibility averaged more than 65%. The decline appeared to be steeper in 1999 than in 1998. Digestibility was generally lowest on Rosana pastures in 1998, but no difference was noted among seeded grasses in 1999.

Crude protein as a percent of diets declined as the grazing season advanced from April to May on Rosana pastures in 1998 and on all pastures in 1999; however, values did not decline to below 11% (Table 6). Crude protein percentages for Hycrest and Luna pastures in June 1998 were equal to April values. Crude protein percentages of Rosana were usually less than Hycrest and Luna, but the differences were not consistently significant (Table 6).

Livestock Performance

Daily gains (Table 7) and gains per hectare (73 $\pm$ 4.2 kg ha⁻¹) were similar among seeded grasses in 1997. Daily gains were greater on Hycrest than Rosana in 1998 (Table 7). This could be related to the greater amount of standing dead observed in the Rosana pastures in spring

Table 4. Means for CP standing crop (seeded species by date interaction); standard error equals ± 27.1 .

Dates	Seeded species		
	Hycrest	Luna	Rosana
----- (kg ha ⁻¹) -----			
1997 May	228 ^{Acd1}	157 ^{Ac}	190 ^{Aab}
June	82 ^{Ae}	62 ^{Ad}	71 ^{Ac}
1998 April	322 ^{Aab}	243 ^{Bab}	260 ^{ABa}
May	359 ^{Aa}	316 ^{Aab}	197 ^{Bab}
June	155 ^{Ade}	139 ^{Ac}	113 ^{Ac}
1999 April	270 ^{Abc}	236 ^{Ab}	207 ^{Aab}
May	212 ^{Bde}	304 ^{Aa}	234 ^{ABa}
June	144 ^{Ae}	167 ^{Ac}	135 ^{Abc}

¹Within a date, species means with the same uppercase superscripts are not different ($P < 0.05$). Within a species, means of dates with the same lowercase superscripts are not different ($P < 0.05$).

Table 5. Means for IVDOM concentrations in diets collected on the experimental pastures in 1998 and 1999; standard error equals ± 1.3 .

Species	1998			1999		
	April	May	June	April	May	June
----- (%) -----						
Hycrest	78 ^{ABb1}	76 ^{Abc}	73 ^{Ac}	83 ^{Aa}	79 ^{Ab}	68 ^{Ad}
Luna	80 ^{Aa}	71 ^{Bb}	72 ^{Ab}	81 ^{Aa}	78 ^{Aa}	67 ^{Ac}
Rosana	76 ^{Bb}	66 ^{Cc}	67 ^{Bc}	83 ^{Aa}	78 ^{Ab}	69 ^{Ac}

¹Within a date, species means with the same uppercase superscripts are not different ($P < 0.05$). Within a species, means of dates with the same lowercase superscripts are not different ($P < 0.05$).

Table 6. Means for crude protein (CP) in diets collected on the experimental pastures in 1998 and 1999; standard error equals ± 1.3 .

Species	1998			1999		
	April	May	June	April	May	June
Hycrest	22 ^{ABa1}	19 ^{Aab}	22 ^{Aa}	21 ^{Aa}	17 ^{ABbc}	14 ^{Ac}
Luna	25 ^{Aa}	16 ^{Bc}	22 ^{Aab}	23 ^{Aa}	19 ^{Abc}	12 ^{Ad}
Rosana	19 ^{Ba}	11 ^{Bb}	14 ^{Bb}	20 ^{Aa}	15 ^{Bb}	14 ^{Ab}

¹Within a date, species means with the same uppercase superscripts are not different ($P < 0.05$). Within a species, means of dates with the same lowercase superscripts are not different ($P < 0.05$).

1998. Gains per hectare were greater for Hycrest 178 ± 7.2 kg ha⁻¹) than for both Luna and Rosana ($\bar{x} = 148 \pm 7.2$ kg ha⁻¹). This may reflect the lowered IVDOM observed for Rosana compared to Hycrest in 1998. Daily gains per head (Table 7) and gains per hectare on Hycrest and Rosana ($\bar{x} = 104 \pm 7.2$ kg⁻¹) were greater than on Luna (72 ± 7.2 kg ha⁻¹) in 1999.

The lack of sensitivity of weight gains to nutritional quality may partially be a reflection of the technique used to measure IVDOM. Addition of N to IVDOM media, as in these analyses, has been shown to mask differences in response to Northern Great Plains forages such that weight gains of steers grazing native rangeland were better predicted by IVDOM media without supplemental N compared to that with N (Blummel et al. 2001).

Steer gains in 1997 and 1998 were 40% greater than heifer gains in 1999 (Table 7). Gains per hectare for Hycrest and Rosana were greatest in 1998, intermediate in 1999, and least in 1997. In contrast, gains per hectare on Luna were greatest in 1998 (152 ± 7.2 kg ha⁻¹), but gains in 1999 (72 ± 7.2 kg ha⁻¹) were similar to those during the shortened grazing period in 1997 ($\bar{x} = 68 \pm 7.2$ kg ha⁻¹).

Discussion

Seedlings of new cultivars are used to increase available forage and to extend the period of high quality forage for grazing livestock (Wasser 1982, Holzworth et al. 2000, Vallentine 1980). Crested wheatgrass has traditionally been used for spring grazing and in some instances autumn grazing (Vallentine 1980). Pubescent wheatgrass is used during the spring and summer (Holzworth et al. 2000). Western wheatgrass, a native to Northern Great Plains rangelands, provides valuable forage during the spring, summer, and autumn (Wasser 1982).

Data from this study and others clearly show that in some years, crested wheat-

grass provides more forage than selected cultivars of native species e.g., western wheatgrass and native range (Smoliak 1968, Hart et al. 1983, Adams et al. 1989) and will allow an increase in livestock numbers. However, this does not occur every year in every region. This occurred in 1 out of 3 years when Hycrest was compared to Rosana, a selected cultivar of western wheatgrass in our study. Willms and Jefferson (1993) reported relative above-ground production of native mixed prairie vs seeded monocultures is not consistent among production years or studies. Others are also concerned about the negative effect introduced plant species, e.g., crested wheatgrass, can have on native species, biodiversity, and soils (Dormaar et al. 1995, Lesica and DeLuca 1996, Christian and Wilson 1999, Krzic et al. 2000). Some results suggest seedings of crested wheatgrass in the Northern Great Plains may reduce biodiversity and alter pools and flows of energy and nutrients in the seeded areas within the prairie ecosystem. Based on these findings, Lesica and DeLuca (1996) cautioned that the continued conversion of native prairie by plowing and planting crested wheatgrass or other exotic species seemed ill advised.

Concerns about the persistence of pubescent wheatgrass in the 335 mm precipitation zone were first raised by Currie and White (1982). During a prolonged drought, they found cultivars of the intermediate-pubescent wheatgrass complex to be killed or to be the most severely damaged of a number of grass species frequently seeded in the Northern Great Plains.

Livestock performance varies among

seeded pastures and native range (Houston and Urick 1972, Hart et al. 1983, Adams et al. 1989, Hofmann et al. 1993). While some report increases in individual animal performance from grazing seeded ranges (Houston and Urick 1972) others report the main advantage of seeded ranges appears to be increased seasonal carrying capacity (Hart et al. 1983, Adams et al. 1989, Hofmann et al. 1993). Adams et al. (1989) imply that animal performance will not differ greatly among seeded pastures and native range in good-to-excellent condition that contains a high component of cool-season perennial grasses. Greater differences may occur when native range contains a higher proportion of warm-season perennial grasses.

Management Implications

Willms and Jefferson (1993) suggested a crucial question is not which species to seed but whether seeding should be done at all on many sites. However, seeding cool-season monocultures on western rangelands provides livestock managers with another tool to increase available forage and provide quality forage for grazing livestock. Choosing the best forage for the intended use is critical. Choosing the best variety becomes more challenging as new varieties are released from both the public and private sectors. Seeding is not a panacea, but many livestock operations can benefit from the use of an integrated management strategy using both rangelands and seeded cool-season monocultures. Learning more about the growth and quality characteristics of new forages is a key first step in developing a successful management strategy which includes seeded forages.

Careful assessment of both the suitability of a planted species for the intended use and the hazard of undesired consequences, e.g., negative impacts on soil and indigenous vegetation, should precede any pasture or rangeland planting. The levels of productivity and persistence of Rosana make this selected native cultivar of west-

Table 7. Means for average daily gain of yearling cattle; standard errors equal ± 0.03 for species, ± 0.08 for year, and ± 0.04 for species by year interaction.

Year	Hycrest	Luna	Rosana	Mean
	----- (kg head ⁻¹ day ⁻¹) -----			
1997	1.13 ^{Aa1}	1.05 ^{Aa}	1.26 ^{Aa}	1.15 ^a
1998	1.28 ^{Aa}	1.09 ^{ABa}	1.03 ^{Bb}	1.14 ^a
1999	0.74 ^{Ab}	0.52 ^{Bb}	0.78 ^{Ac}	0.68 ^b
Mean	1.05 ^A	0.89 ^B	1.03 ^A	

¹Within a date, species means with the same uppercase superscripts are not different ($P < 0.05$). Within a species, means of dates with the same lowercase superscripts are not different ($P < 0.05$).

ern wheatgrass a viable option when managers prefer using natives. However, the potential for greater animal gain in some environmental conditions (1998) confirms that Hycrest crested wheatgrass can be a useful forage plant for livestock production in the region. Based on the encroachment of invading species, persistence of Luna is marginal in the 335-mm precipitation zone in the Northern Great Plains.

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Evaluation of habitat structural measures in a shrubland community

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Abstract

Accurate and efficient monitoring of habitat structure on rangelands is important for understanding wildlife responses to land management practices. Unfortunately, studies of wildlife responses to changes in habitat structure often use monitoring techniques that fail to measure variation in multiple structural dimensions. Our objectives were to evaluate relationships between measures of habitat structure in a shrubland community and to discuss the usefulness of several techniques in integrating multiple structural dimensions into a single index of habitat structure. We evaluated relationships between shrub cover, herbaceous cover, shrub patch number, average shrub patch size, average vegetation height, visual obstruction across multiple strata of a profile board, cone of vulnerability, and angle of obstruction using a principle component analysis. Many of these variables were redundant with each other. Average visual obstruction estimates, using a profile board, were associated with variability in vertical structure as indicated by its association with height. Coefficients of variation for cone of vulnerability and visual obstruction were dependent upon their means and of limited use in describing horizontal patchiness. In contrast, shrub patch number was not linearly correlated with any other single measure in our analysis, and may be useful in describing horizontal patchiness. Cone of vulnerability and angle of obstruction are recently developed techniques that provided useful, single indices of multidimensional habitat structure. Efficient monitoring of wildlife habitat structure should employ multiple, independent techniques that measure distinct dimensions of habitat structure or a single measure that integrates multiple dimensions.

Key Words: cone of vulnerability, gallinaceous bird, sand shinnery, vegetation structure, visual obstruction, patchiness, heterogeneity

Monitoring techniques are critical for evaluating the ecological effects and efficacy of rangeland management practices. Many measures of vegetation structure have been developed on rangelands as an index of rangeland productivity (Robel 1970, Ganguli et al. 2000, Vermeire and Gillen 2001). The conservation of sen-

Resumen

El monitoreo eficiente y certero de la estructura del hábitat es importante para entender la respuesta de la fauna silvestre a las prácticas de manejo del terreno. Desafortunadamente los estudios de la respuesta de la fauna silvestre a los cambios de estructura del hábitat a menudo usan técnicas de monitoreo que fracasan en medir la variación en dimensiones estructurales múltiples. Nuestros objetivos fueron evaluar las relaciones entre medidas de la estructura del hábitat en una comunidad de arbustivas y discutir la utilidad de varias técnicas en integrar las dimensiones estructurales múltiples en un solo índice de estructura del hábitat. Con el uso del análisis de componentes principales evaluamos las relaciones entre la cobertura de arbustos, la cobertura de herbáceas, el número de parches de arbustos, el tamaño promedio de los parches de arbustos, la altura promedio de la vegetación, la obstrucción visual a través de los estratos múltiples de un perfil amplio, el cono de vulnerabilidad y el ángulo de obstrucción. Muchas de estas variables fueron redundantes unas con otras. Las estimaciones promedio de la obstrucción visual, usando un perfil amplio, estuvieron asociadas con la variabilidad en la estructura vertical, tal como lo indicó su asociación con la altura. Los coeficientes de variación para la vulnerabilidad del cono y la obstrucción visual fueron dependientes de sus medias y de uso limitado en describir los parches horizontales. En contraste, en nuestro análisis, el número de parches de arbustos no estuvo linealmente correlacionado con ninguna otra de las medidas y puede ser útil en describir la distribución horizontal de los parches. El cono de vulnerabilidad y el ángulo de obstrucción son técnicas recientemente desarrolladas que proveen índices sencillos de la estructura multidimensional del hábitat. El monitoreo eficiente de la estructura del hábitat de la fauna silvestre debe emplear múltiples técnicas independientes que midan distintas dimensiones de la estructura del hábitat o una sola medida que integre las dimensiones múltiples.

sitive wildlife species, such as grouse in western North America, has elevated the importance of monitoring wildlife habitat on rangelands (Applegate and Riley 1998, Nelle et al. 2000). Quantifying vegetation structure is crucial to identifying wildlife habitat (Rotenberry and Wiens 1980, Schulte and Niemi 1998, Sutter and Brigham 1998). Vegetation structure has been identified as a key habitat feature for gallinaceous birds in particular (Guthery 1996). Habitat structure affects animal species composition and abundance directly through mechanical effects such as providing nesting cover (Townsend et al. 2001) and indirectly through changes in microclimate (Bell et al. 1991). However, precise definitions of habitat structure are difficult to obtain.

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Many papers focused on wildlife habitat avoid definitions of habitat structure entirely or in part because of confusion over relationships between typical measures of structure (Verner et al. 1986). Other studies simply define it in terms of juxtaposition of vegetation features to explain habitat structure (Bookhout 1994). Guthery (1996) stated that "structure refers to the height, density, biomass, and dispersion of herbaceous and woody vegetation." Rotenberry and Wiens (1980) defined habitat structure as the physical configuration of a terrestrial environment provided by vegetation. Some attempts to define habitat structure describe 2 dimensions, vertical and horizontal, which dictate this physical configuration of vegetation in space (Smith 1986). However, explanations of the relationships between horizontal and vertical dimensions of habitat structure have been imprecise, and there is little information evaluating the appropriateness of individual measurement techniques in consolidating these dimensions (Rotenberry and Wiens 1980).

Techniques used to monitor habitat structure are diverse, and minimal descriptions of relationships between different techniques often result in redundant habitat evaluations. Traditional sampling techniques, such as line-intercept methods, often focus on estimates of cover provided by various plant functional groups, which are often well correlated with structure (Bonham 1989). Tools, such as profile boards and Robel poles (Robel et al. 1970), can provide measures of structure in different vegetation communities by estimating visual obstruction (Guthery et al. 1981). Coefficients of variation of these techniques are often used as indicators of horizontal heterogeneity (Roth 1976, Madden et al. 1999). Other approaches to measuring horizontal heterogeneity, such as landscape level investigations, focus on variably-scaled spatial patterns in communities (McGarigal and McComb 1995). Recently, a 3-dimensional technique, the cone of vulnerability (Kopp et al. 1998), was developed in an attempt to collapse infinitely diverse structural features into a single index (F. S. Guthery, Okla. State Univ., pers. commun.). All of these techniques vary as to the dimension and proportion of variation in habitat structure explained, yet few studies have evaluated the relationships between different approaches. Furthermore, it is important to search for sampling techniques that measure multiple dimensions and integrate them into a single index of habitat structure (Rotenberry

and Wiens 1980). Our objectives were to: (1) evaluate relationships between measures of habitat structure in a shrubland community, and (2) discuss the usefulness of several techniques in integrating multiple structural dimensions into a single index of habitat structure.

Materials and Methods

Study Area

Study sites were located on the Black Kettle National Grasslands (BKNG) in Roger Mills County, Okla. and adjacent private land in Hemphill County, Tex. (35°37'N, 100°40'W). Sample sites were chosen within available sand shinnery oak (*Quercus havardii* Rydb.) communities. Sites on the National Grasslands had prescribed fire histories ranging from unburned to burned within 1 growing season prior to sampling. Private land had a history of herbicide applications to reduce shrub cover. This variable management history led to a wide range of structural variation among sites.

Sand shinnery communities are the largest of the oak (*Quercus* spp.) communities found in the United States, occupying about 2–3 million ha in the southern Great Plains (Peterson and Boyd 1998). These oak communities are only 0.25–1.5 m tall and are classified as shrublands. Sand shinnery oak is the dominant species, with sand sagebrush (*Artemisia filifolia* Torr.) codominating. Common grasses include sand bluestem (*Andropogon gerardii* var. *paucipilus* Nash), little bluestem (*Schizachyrium scoparium* Nash), and sideoats grama (*Bouteloua curtipendula* Torr.). Nomenclature follows Hatch et al. (1990). Sand shinnery communities support a wide variety of wildlife species including mule deer (*Odocoileus hemionus* Rafinesque), white-tailed deer (*O. virginianus* Boddaert), pronghorn antelope (*Antilocapra americana* Ord), peccary (*Dicotyles tajacu* L.), lesser prairie-chickens (*Tympanuchus pallidicinctus* Ridgeway), northern bobwhites (*Colinus virginianus* L.), Rio Grande turkeys (*Melagris gallopavo intermedia* L.), mourning doves (*Zenaidura macroura* L.), and various species of songbirds, lagomorphs, rodents, reptiles, and invertebrates (Peterson and Boyd 1998).

All sites sampled were grazed by cattle at 1.5 ha/AUM. The BKNG is not contiguous, but consists of a series of land fragments ranging in size from 10 to 500 ha (Burgess et al. 1963). The climate of the region is semiarid, with mean August and

January temperatures of 28.0 and 2.7° C, respectively. The area has an average growing season of 209 days and average annual precipitation of 65 cm (Burgess et al. 1963). Precipitation is highly variable and bimodally distributed with peaks in May–June and August–September. Topography of the area consists of rolling hills, with elevation ranging from 518 to 793 m above sea level.

Sampling Methods

We measured habitat structure during the growing seasons (June–August) of 1998 and 1999. Eighty-four, 100-m line transects were used to measure canopy cover of woody and herbaceous plants (Bonham 1989). Since shrubs were the dominant vegetation cover type, shrub cover was measured as an absolute value along the transect, with herbaceous cover recorded only in the absence of shrub cover. Minimum resolution used to define plant functional group cover along the transect was 10 cm. This sampling resolution was used so that fine-scale changes in structure that may be important to some wildlife species could be detected. Shrub patch number (#/100 m) and average size of shrub patches (cm) were determined from the line transect data by summing the number of distinct shrub patches and averaging their linear lengths. Distinct shrub patches could be as small as 10 cm and were defined as continuous shrub cover if there were no canopy breaks greater than 10 cm. Vegetation height was measured every 1 m along the transect. If no vegetation was present at that point, height was recorded as 0. We estimated visual obstruction every 10 m along the transect using a profile board as described by Nudds (1977) and modified for sand shinnery communities by Guthery et al. (1981). The 6.8-cm wide profile board had 12 strata, each stratum being 10 cm tall. Estimates were taken perpendicular to the line transect at a distance of 7 m, with the observer kneeling at a height of 1.5 m over the transect. Percent visual obstruction was estimated for each stratum.

We measured the cone of vulnerability (Kopp et al. 1998) every 10 m along the transects. The cone of vulnerability is a 3-dimensional view of visual obstruction and has been identified as a measure that quantifies habitat structure important for northern bobwhites (Kopp et al. 1998). We assessed the cone of vulnerability by measuring angles in 8 directions (N, NE, E, SE, S, SW, W, NW) from a point located 10 cm above the ground to the top of the nearest obstructing vegetation. We

Fig. 1. Depiction of measurement components to determine cone of vulnerability (an integration of vertical and horizontal dimensions of habitat structure) where: v = height of obstruction (vertical structure), h = distance from random point to base of obstruction (horizontal structure), c = line used to determine angle of obstruction, A = angle of obstruction (arcsine h/c). Adapted from Kopp et al. (1998).

considered the average of the 8 angles for each point to be the angle of obstruction. We then used the angle of obstruction to calculate the volume of the air space included within a cone (Kopp et al. 1998). A larger cone of vulnerability equates to a structurally more open habitat. The angle of obstruction used in determining the cone of vulnerability is formed by 2 basic components, height of nearest obstructing plant and distance from the point of measure to the plant (Fig. 1). These components suggest the potential of this measure to integrate the vertical and horizontal dimensions of habitat structure.

Statistical Analysis

We conducted a principal components analysis (PCA) on data from 84 transects using CANOCO software (Ter Braak and Smilauer 1998) to assess the relationships among the structural measures, identify structural variables that were redundant, and determine the percent of structural variation explained by various measures of habitat structure. The variables for each transect included in the PCA were shrub cover, herbaceous cover, mean cone of vulnerability, mean angle of obstruction, mean shrub patch size, shrub patch number, mean vegetation height, percent visual obstruction of stratum 1 through stratum 12, the mean of all visual obstruction values, and the coefficient of variation (CV) for the cone of vulnerability, angle of obstruction, height, and visual obstruction measures. We analyzed the cone of vulnerability and angle of obstruction sep-

several meaningful variables, verify our PCA, and obtain probability values. We determined the best-fit line by choosing the model that maximized the r^2 and minimized MSE.

Results

Variability within our data was reflective of the diverse management histories present at our study sites. Mean shrub cover was 50% (4 to 86%). Mean average height of vegetation along each transect was 38 cm (13 to 88 cm). Mean shrub patch number was 95/100 m (13 to 166/100 m). Mean cone of vulnerability was 0.667 m^3 (0.019 to 1.782 m^3).

Variation in structure explained by PCA axis 1 and PCA axis 2 was 57.9 and 17.4%, respectively, resulting in a cumulative total of 75.3%. Axes 3 and 4 of the PCA explained less than 10% of the variation using the variables that we measured. Measures typically associated with vertical structure, such as mean visual obstruction and mean vegetation height, had high component scores on PCA axis 1 and relatively low component scores on PCA axis 2 (Table 1). Variables that were associated with PCA axis 1 and PCA axis 2 included mean cone of vulnerability, cone of vulnerability CV, mean angle of obstruction, angle of obstruction CV, mean shrub patch

Table 1. Component scores and correlation coefficients of habitat structural variables for sand shinnery communities in Oklahoma and Texas, 1998–1999. Component scores reflect degree of correlation with vertical (axis 1) and horizontal (axis 2) habitat structure represented by 2 orthogonal axes of a principal component analysis (PCA).

Habitat Variable	PCA Axis 1 Scores	PCA Axis 2 Scores	Shrub Cover (r)	Shrub Patch Number (r)
Shrub cover	0.840**	-0.340**		0.391**
Herbaceous cover	-0.765**	0.245*	-0.838**	-0.510**
Height	0.886**	0.112	0.732**	-0.036
Height (CV)	-0.312**	0.449**	-0.410**	-0.103
Cone of vulnerability	-0.864**	0.387**	-0.896**	-0.402**
Cone of vulnerability (CV)	0.822**	-0.167	0.765**	0.072
Angle of obstruction	0.881**	-0.351**	0.883**	0.335**
Angle of obstruction (CV)	-0.679**	0.390**	-0.742**	-0.387**
Visual obstruction	0.955**	0.252*	0.675**	-0.026
Visual obstruction (CV)	-0.516**	0.478**	-0.552**	-0.222*
Stratum 1	0.441**	-0.468**	0.386**	0.290**
Stratum 2	0.612**	-0.478**	0.540**	0.288**
Stratum 3	0.810**	-0.407**	0.739**	0.359**
Stratum 4	0.892**	-0.297**	0.809**	0.301**
Stratum 5	0.921**	-0.062	0.752**	0.115
Stratum 6	0.918**	0.170	0.672**	-0.025
Stratum 7	0.862**	0.398**	0.556**	-0.154
Stratum 8	0.822**	0.507**	0.487**	-0.202
Stratum 9	0.784**	0.582**	0.438**	-0.211
Stratum 10	0.739**	0.611**	0.390**	-0.203
Stratum 11	0.709**	0.605**	0.394**	-0.200
Stratum 12	0.676**	0.584**	0.394**	-0.191
Shrub patch size	0.790**	0.189	0.730**	-0.282**
Shrub patch number	0.125	-0.655**	0.391**	

** $P < 0.01$, * $P < 0.05$

Fig. 2. Principal components analysis of vertical and horizontal structural relationships among habitat variables for sand shinnery communities in Oklahoma and Texas, 1998–1999. Arrows pointing opposite of one another depict negative relationships, arrows pointing in the same direction depict positive relationships, and arrows at right angles depict orthogonality. Strata 1–12 (S1– S12) represent individual stratum along a profile board from ground level to 120 cm at 10-cm intervals. Shrub refers to cover.

size, shrub cover, herbaceous cover, and strata 3–11 of the profile board (Table 1, Fig. 2). Most of these structural measures were highly correlated with each other (Table 1).

Shrub cover had high positive correlations with mean shrub patch size, mean vegetation height, cone of vulnerability CV, mean angle of obstruction, and strata 3–5 of the profile board (Table 1). Mean cone of vulnerability, angle of obstruction CV, and herbaceous cover had high negative correlations with shrub cover (Table 1). The CVs for angle of obstruction and cone of vulnerability had a strong negative correlation ($r = -0.737$, $P < 0.01$; $r = -0.837$; $P < 0.01$) which indicated disagreement with each other as to the spatial variability within this community.

Shrub patch number had the highest component score on PCA axis 2 and low linear correlations with the other variables in our analysis (Table 1). When a second order polynomial regression was applied, shrub patch number had a quadratic relationship with shrub cover (Fig. 3). Shrub cover, herbaceous cover, angle of obstruction, cone of vulnerability, and strata 7–11 of the profile board had relatively high component scores for both axes which indicated these variables may be correlated with more than 1 dimension of structure (Table 1, Fig. 2).

Discussion

Past studies have either failed to identify the dimension (vertical or horizontal) of vegetation structure measured or have measured structure in a single dimension (Haensly et al. 1987, Goguen and Mathews 1998, McKee et al. 1998). For clear and efficient descriptions of habitat structure, multiple measures of habitat structure should be independent and measure distinct structural attributes. When single measures are used, it is important that they integrate multiple dimensions. Our data suggested that many commonly used measures of habitat structure are redundant. Many measures in our analysis were related to vertical structure, as indicated by their association with height in the PCA. Several of the measures evaluated in this study, such as cone of vulnerability, angle of obstruction, and the profile board, have the potential to integrate vertical and horizontal structure into a single index of habitat structure.

Horizontal structure is often defined in terms of habitat patchiness or porosity (Forman and Godron 1986, Bell et al. 1991). Patchiness is often a more accurate predictor of bird species diversity than vertical variability (MacArthur et al. 1962, Roth 1976). Shrub patch number and strata

8–12 of the profile board explained the most variation on axis 2, were not strongly correlated with other measures, and may be the best indicators of horizontal variability in these shrubland communities. Shrub patch number was the least redundant measure in our analysis, indicating that this measure may be useful in future assessments. Physical characteristics of vegetation, such as shrub patch number, that measure attributes related to horizontal structure are often evaluated at the landscape level (Forman and Godron 1986, McGarigal and McComb 1995), but rarely at a habitat-patch level as we did in our study.

Coefficient of variation for height or visual obstruction has been used as a measure of horizontal patchiness (Roth 1976, Madden et al. 1999). However, coefficient of variation only measures variation around a mean, rather than spatially explicit horizontal variation such as that measured with shrub patch number. In fact, the cone of vulnerability CV suggests that the greatest amount of horizontal variability occurred at high levels of shrub cover, whereas the angle of obstruction CV indicated that the greatest horizontal variability occurred at low levels of shrub cover. The discrepancy between these CVs occurs because of the formulas required to convert the angle of obstruction into an area-based measure. The means of these measures are also negatively correlated, indicating that patterns of the CVs are indeed dependent upon the mean and of limited use in describing horizontal patchiness. In contrast, relationships of shrub patch number with shrub cover, as well as landscape-level models, suggest that the greatest amount of horizontal variability should occur at intermediate levels of shrub cover (Fig. 3; Hargis et al. 1997).

Estimating visual obstruction using density or profile boards with multiple strata has been employed as a method to quantify structural density of vegetation. Our data suggested that average visual obstruction, which is frequently used as a single index of habitat structure (Nudds 1977, Guthery et al. 1981, DeFazio et al. 1988), is redundant with height; and therefore, was interpreted primarily as a measure of vertical structure. However, examining the 12 individual strata of the profile board independently gave a wide range of information, which was not gained from any other measure. An important limitation in quantifying vegetation structure using visual obstruction is associated with data analysis. To analyze data from a profile

Fig. 3. Quadratic relationship between shrub patch number and percent shrub cover from 84 line transects in sand shinnery communities of Oklahoma and Texas, 1998-1999. Shrub patch number and shrub cover were taken at 10-cm intervals along 100-m line transects.

board without violating statistical assumptions of independence, each stratum should be considered dependent on the lower strata. This results in a complex vector of interdependent variables instead of a single univariate index of vertical and horizontal structure.

The angle of obstruction and cone of vulnerability are recently developed techniques that have potential to integrate multiple dimensions of habitat structure. Cone of vulnerability is calculated from the angle of obstruction (A), which is a function of plant height (v) and the ground distance (h) of the plant from a point in space, indicating that it is a direct mathematical integration of vertical and horizontal dimensions of habitat structure (Fig. 1). The PCA supported this, suggesting that the cone of vulnerability and angle of obstruction were correlated with both axes. A recent model suggests that an ideal landscape for northern bobwhites would be comprised of an average cone of vulnerability of 0.691 m³, shrub cover of 53%, and relatively high variability (CVs >50%) (Kopp et al. 1998). A technique, such as the cone of vulnerability or angle of obstruction, that integrates multiple components of habitat structure could be used as a measure of overall structural heterogeneity in shrubland communities, but the coefficient of variation may be of little added value.

Various habitat management practices influence the vertical and horizontal dimensions of vegetation structure differently, yet studies often measure only a single dimension of structure. Choosing multiple techniques that are not redundant with each other and measure distinct dimensions of habitat structure or a single measure that integrates multiple dimensions is crucial in the design of efficient monitoring studies. The cone of vulnerability and angle of obstruction appear to effectively integrate multiple dimensions of habitat structure in sand shinnery communities. Individual strata along a profile board also provided information about multiple structural dimensions. Shrub patch number provided data that was not related to other measures in our analysis, and would be useful in future habitat evaluations.

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A robust model for estimating standing crop across vegetation types

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Abstract

Some recent investigations have shown the visual obstruction (VO) measurement method to be an effective means of estimating herbage standing crop non-destructively in tallgrass prairie. Although the method is rapid and inexpensive, visual obstruction models have been limited to tallgrass prairie and sandhills range types. Our primary objective was to evaluate the relationships between visual obstruction and standing crop in shortgrass plains and mixed prairie. Secondly, we wanted to determine whether these models could be integrated with tallgrass prairie models without appreciable losses in prediction capabilities. We conducted 44 trials on non-burned sites with various levels of grazing pressure. Each trial was composed of 20 randomly selected plots and served as 1 experimental unit to represent pasture-level standing crop estimation. Visual obstruction readings were taken from a modified Robel pole placed centrally at the back of 0.1-m² quadrats and vegetation was clipped to estimate standing crop. Trial standing crop was regressed on visual obstruction and models were compared among range types. Visual obstruction explained 91 and 89% of the variation in shortgrass plains and mixed prairie standing crop, respectively. A single visual obstruction model effectively estimated herbage standing crop across range types and produced a coefficient of determination of 0.93. Although greater precision may be obtained from models developed for specific sites, the ability of a single visual obstruction model to predict standing crop across years, management schemes, and range types indicates visual obstruction models may be successfully employed on a regional basis.

Key Words: mixed prairie, non-destructive sampling, Robel pole, shortgrass, tallgrass

Herbage standing crop is commonly monitored on rangelands to determine stocking capacity and effects of management or experimental treatments. Measurements are typically made by clipping vegetation from randomly-placed quadrats and extrapolating dry weight over the area of interest. Clipping can provide accurate and precise estimates, but the time and labor required often prevent researchers and managers from clipping or collecting an adequate number of samples.

Indirect methods have been tested to simplify standing crop estimation, but accuracy is generally sacrificed and the applicability of individual models is typically limited relative to direct

Resumen

Recientes investigaciones han mostrado el método de medida de obstrucción visual (VO) como un medio efectivo y no-destructivo para la estimación de la producción de forraje en pastizales de zacates altos. Aunque el método es rápido y barato, los modelos de VO han sido limitados a pastizales de zacates altos y pastizales de colinas arenosas. Nuestro objetivo principal fue evaluar la relación entre VO y la producción de forraje en pastizales de zacates cortos y pastizales mediano abierto. También quisimos determinar si estos modelos pudieran ser integrados a los modelos de pastizal de zacates altos sin pérdida apreciable en la capacidad de predicción. Se realizaron 44 muestreos en sitios no quemados con diferentes niveles de carga animal. Cada muestreo consistió como la parcela experimental consistió de 20 parcelas seleccionadas al azar, representando la estimación de producción de forraje en cada nivel. Las lecturas de VO fueron tomadas desde un poste Robel modificado colocado en el centro atrás de los cuadrantes de 0.1 m² y se realizaron cortes para estimar la producción de forraje. La producción de forraje de los muestreos fue analizada con datos de VO a través de regresión y los modelos fueron comparados entre tipos de pastizal. Un modelo estimó efectivamente la producción de forraje a través de tipos de pastizal, con coeficiente de determinación de 0.93. La habilidad de un solo modelo VO para predecir productividad a través de los años, esquemas de manejo, y tipos de pastizal indica que modelos VO puede ser empleado exitosamente en una base regional.

measurements (Michalk and Herbert 1977, Gonzalez et al. 1990, Catehpole and Wheeler 1992, Hannoney et al. 1997). Visual obstruction (VO) measurements were highly correlated with standing crop in homogeneous tallgrass communities (Robel et al. 1970). Vermeire and Gillen (2001) also found VO measurements to improve sampling efficiency and effectively estimate standing crop year-round in heterogeneous tallgrass prairie, across seral stages and levels of standing crop.

Evaluation of the VO method has been limited to tallgrass prairie, sandhills, and sandy lowland range types. Higgins et al. (1996) suggested the method would not provide useful information in shortgrass plains or sparsely vegetated habitats. Volesky et al. (1999) also stated that the VO method was of limited utility in sandhills vegetation. However, the VO method was successfully employed on sandy lowlands in Nebraska (Benkobi et al. 2000) and under a wide array of conditions in southern tallgrass prairie (Vermeire and Gillen 2001), suggesting the method may

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be applicable for pasture standing crop estimation in other vegetation types.

Our objectives were to evaluate the relationships between VO and standing crop in shortgrass plains and mixed prairie and determine whether these models could be integrated with a tallgrass model to produce a more universal equation (Vermeire and Gillen 2001) without appreciable loss in pasture-level prediction capabilities.

Methods and Materials

Study Areas

Shortgrass plains trials were conducted from July through August 1999 in Armstrong County, Tex. (35° 10' N, 101° 15' W, elevation 975 m). The climate is dry steppe with an average frost-free growing period of 181 days. Mean annual precipitation is 505 mm with 75% occurring from April to September (NOAA 1998). Sampling was conducted on deep hardland and shallow range sites with Pullman silty clay loam (Fine, mixed, superactive, thermic Torrtic Paleustolls) and Potter soils (Loamy-skeletal, carbonatic, thermic Petronodic Ustic Haplocalcids), respectively (Jacquot et al. 1965). The area was moderately stocked with cows and calves under a continuous year-long grazing system.

Dominant grasses were buffalograss [*Buchloe dactyloides* (Nutt.) Engelm.] and blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Steud], with threeawns (*Aristida* spp. L.), and sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.] as secondary components. Dominant forbs included woolly plantain (*Plantago patagonica* Jacq.), prairie coneflower [*Ratibida columnifera* (Nutt.) Woot. & Standl.], annual broomweed [*Amphiachyris dracunculoides* (DC.) Nutt. ex Rydb.], and broom snakeweed [*Gutierrezia sarothrae* (Pursh) Britt. & Rusby]. More than 80% of the biomass was comprised of blue grama and buffalograss.

Mixed prairie data were collected from June through August 1999 in Lubbock County, Tex. (33° 35' N, 101° 53' W, elevation 990 m). The climate is dry steppe with an average frost-free growing period of 210 days. Mean annual precipitation is 450 mm with 67% of the precipitation occurring from May to September (NOAA 1998). Sampling was conducted on clay loam and sandy loam range sites with Acuff (Fine-loamy, mixed, superactive, thermic Aridic Paleustalfs) and Amarillo (Fine-loamy, mixed, superactive, thermic Aridic Paleustalfs) soils (Blackstock 1979). Vegetation on the study area had

not been grazed by large herbivores since November 1982, but some of the areas had been mowed.

Dominant grasses included blue grama, purple threeawn (*Aristida purpurea* Nutt.), silver bluestem [*Bothriochloa laguroides* (DC.) Herter], and buffalograss. Other common midgrasses included sand dropseed [*Sporobolus cryptandrus* (Torr.) Gray], Arizona cottontop [*Digitaria californica* (Benth.) Henr], vine mesquite (*Panicum obtusum* H.B.K.), and sideoats grama. Blueweed sunflower [*Helianthus ciliaris* DC.], prairie coneflower, and lambsquarters (*Chenopodium album* L.) were the dominant forbs.

Tallgrass prairie trials were conducted in Payne County, Okla. (36° 04' N, 97° 13' W, elevation 280 m) from 1994 to 1996 (Vermeire and Gillen 2001). The continental climate allows a 204-day frost-free growing season from April to October. Mean annual precipitation is 831 mm, with 65% falling as rain from May to October (Myers 1982). Range sites sampled included sandy savannah, loamy prairie, shallow prairie, and eroded prairie. All sites were exposed to cattle grazing at various stocking rates under short-duration, intensive-early stocking, and continuous season-long grazing systems.

Dominant grasses were big bluestem (*Andropogon gerardii* Vitman), little bluestem, Indiangrass [*Sorghastrum nutans* (L.) Nash], and tall dropseed [*Sporobolus asper* (Michx.) Kunth]. Western ragweed (*Ambrosia psilostachya* DC.) and annual broomweed were the dominant forbs. Grama grasses (*Bouteloua* spp. Lag.), annual threeawn (*Aristida oligantha* Michx.), and forbs were more prominent on sites in lower seral stages.

Methods

We conducted 44 trials on non-burned sites in mixed prairie ($n = 24$) and shortgrass plains ($n = 20$) over a wide array of standing crops and species composition. Plant phenology was also variable among trials because data were collected weekly from June through August, covering early-leaf to mature plant stages. Each trial consisted of 20 individual plots (20 x 50-cm quadrats) arranged systematically along pace transects, with approximately 15 m between plots.

Visual obstruction was measured with a visual obstruction pole (Robel et al. 1970). The measurement pole was a wooden dowel (2.5 x 100 cm) marked with alternating red and white decimeter bands. The pole also was marked with black lines every 2 cm. A second wooden dowel (1 x

100 cm) was attached to the measurement pole by a 4-m string to maintain a consistent observation point. The visual obstruction pole was placed centrally at the distant short side of each 20 x 50-cm quadrat and observed from a distance of 4 m and a height of 1 m. A single reading was taken at each plot by recording the height of the lowest visible black mark. All vegetation rooted in the plot was then clipped to ground level and oven-dried to a constant weight at 55° C to determine standing crop.

Relationships between standing crop and visual obstruction were determined by regression analysis, using trial means as observations (SAS 1985). Trials were selected as experimental units to address the objective of assessing pasture-level standing crop estimation and to reduce bias created by relating visual obstruction (VO) to quadrats of fixed dimensions (Vermeire and Gillen 2001). Indicator regression was used to identify differences in models by range type (Neter et al. 1990). Root mean squared errors (RMSE) were used to assess model accuracy and model precision was evaluated by constructing 95% confidence intervals (Zar 1974). Prediction intervals were calculated for future observations and means of 2, 4, and 6 future observations to indicate with 95% confidence the intervals within which future users of the models may expect their true values to lie relative to model predictions (Neter et al. 1990). Smallest, largest, and mean maximum estimate errors are provided to indicate the range and mean differences between estimates and limits for confidence intervals and prediction intervals.

Results and Discussion

Trial standing crop ranged from 1,820 to 5,360 kg ha⁻¹ in mixed prairie and 800 to 1,990 kg ha⁻¹ in shortgrass plains. Visual obstruction (VO) was positively related to standing crop and explained at least 89% of the variation in standing crop for mixed prairie ($P < 0.01$) and shortgrass plains ($P < 0.01$, Fig. 1). Similar results were obtained in non-burned tallgrass prairie (Robel et al. 1970, Vermeire and Gillen 2001) and a sandy lowland range site (Benkobi et al. 2000). The accuracy of both models would comply with most management and research needs (Table 1). Confidence intervals indicated the true mean standing crop at any level of VO within our range of data would be expected to occur within 121 kg ha⁻¹ of our esti-

Fig. 1. Relationships between standing crop and visual obstruction in shortgrass plains and mixed prairie and 95% prediction intervals for single future observations.

mate in shortgrass plains and 365 kg ha⁻¹ in mixed prairie.

Prediction intervals showed with 95% confidence that the true standing crop for any single trial observation made in the future would be expected to occur within 197 kg ha⁻¹ of the shortgrass model estimates and within 864 kg ha⁻¹ of mixed prairie model estimates (Fig. 1). Although both models were accurate and the estimated values were precise, reliable estimates may not be expected with a single future trial.

As with any sampling, increasing sample size will increase confidence in estimates and reduce the size of intervals within which future observations are expected to lie. Vermeire and Gillen (2001) determined 6 VO measurements could be taken in the time required to clip 1 plot. Randomly taking 6 times as many VO readings over the same area would closely approximate the mean of 6 trials and reduce mean maximum estimate errors for predicted values to about 79 kg ha⁻¹ in shortgrass plains and 390 kg ha⁻¹ in mixed prairie (Table 2). It is important to recall future data are independent of the data used in the construction of our models and have no effect on model accuracy or precision. Prediction intervals simply provide a measure of expected precision for samples collected in the future.

Prediction model differences occurred among range types ($P = 0.02$). Tallgrass and shortgrass models were very similar. The mixed prairie model differed from the

other habitat types and we believe 2 factors were primarily responsible, plant morphology and management history. Purple threeawn was one of the dominant species and tended to have a weeping canopy structure, providing more herbage mass nearer the soil surface. Additionally, 13 of the 24 trials in mixed prairie were in pas-

tures that had not been grazed or burned for 17 years. The accumulation of standing dead in rested or lightly stocked pastures would increase the herbage mass per unit of visual obstruction. Vermeire and Gillen (2001) showed that the amount of herbage per cm of visual obstruction is reduced on burned sites because much or all of the standing dead vegetation is consumed by fire. Similar effects may occur in heavily grazed pastures if limited amounts of standing dead are retained between years. The slope of our mixed prairie model was nearly identical to that obtained by Benkobi et al. (2000), but the management history of their sites was not stated. Despite the model differences among range types, prediction capabilities were maintained after combining data from pastures in tallgrass prairie, mixed prairie, and shortgrass plains (Fig. 2). A single model explained 93% of the variation in standing crop across range types and produced a root mean squared errors (RMSE) of 380 kg ha⁻¹ ($P < 0.01$). The model containing only tallgrass data had a coefficient of determination of 0.90 and a RMSE of 418 kg ha⁻¹ (Vermeire and Gillen 2001). Because error variances were heterogeneous for the combined model, meaningful confidence intervals and prediction intervals could not be calculated. However, the high coefficient of determination and small standard error for the slope (5.72) indicate the model will pro-

Table 1. Visual obstruction regression coefficients and statistics for shortgrass plains and mixed prairie.

	Shortgrass plains (n = 20)	Mixed prairie (n = 24)
Slope	162 (12) ^a	240 (18)
Intercept ^b	496 (55)	-535 (318)
Root mean square error	74	378
Coefficient of determination (r^2)		
Maximum estimate error ^c	----- (kg ha ⁻¹) -----	
Smallest	35	160
Largest	121	365
Mean	46	219

^aStandard errors for regression coefficients are in parentheses.

^bThe intercept for the mixed prairie model did not differ from 0 ($P = 0.11$).

^cRange and mean maximum estimate errors were calculated from 95% confidence intervals.

Table 2. Maximum estimate errors from 95% prediction intervals on shortgrass plains and mixed prairie visual obstruction models at various sampling intensities.

	Shortgrass plains			Mixed prairie		
	Smallest	Largest	Mean	Smallest	Largest	Mean
	----- (kg ha ⁻¹) ^a -----					
Single trial	160	197	164	799	864	815
2-trial mean	116	164	120	576	663	598
4-trial mean	86	144	91	423	536	451
6-trial mean	73	137	79	357	486	390

^aDifference between estimate and confidence limit from 95% prediction intervals.

Fig. 2. Relationship between standing crop and visual obstruction across tallgrass prairie, mixed prairie, and shortgrass plains vegetation types.

vide reliable estimates, given adequate sampling.

Visual obstruction (VO) has generally been a good predictor of herbaceous standing crop (Robel et al. 1970, Benkobi et al. 2000, Ganguli et al. 2000, Vermeire and Gillen 2001). However, Volesky et al. (1999) had coefficients of determination of 0.31 to 0.41 in Nebraska sandhills vegetation and found no improvement by using trial means as observations. We believe differences among studies can be attributed to sampling procedures. Vermeire and Gillen (2001) found that the area truly measured by VO is 3-dimensional and variable among points. This source of variation in model development can be reduced by designing quadrats to measure only the vegetation affecting the VO reading and by using means of VO readings and clipped estimates as observations. Researchers using rectangular quadrats with the obstruction pole placed at the distant short side have found strong relationships between VO and standing crop using trial means as observations and taking a single reading per quadrat (Robel et al. 1970, Ganguli et al. 2000, Vermeire and Gillen 2001). Those using circular quadrats with the obstruction pole placed centrally have obtained poorer results unless multiple readings were taken from various angles around each quadrat (Volesky et al. 1999, Benkobi et al. 2000).

We found the combined and individual range type models to be accurate. Selecting the appropriate model will

depend on the objectives of the user and the characteristics of their sites. Visual obstruction models are expected to be more accurate and precise if they are developed for individual range types or specific sites, given equal sample size. However, the general applicability of a model is reduced as the associated conditions of that model become more discrete. One advantage of a combined model across range types is that it could be used to estimate standing crop on sites with multiple or interspersed range types. Additionally, a combined model may facilitate use of the VO method for user groups that operate on a regional basis by providing a single universal equation.

Our combined model effectively predicted standing crop year-round across multiple years, range types, range sites, seral stages, and management systems. If greater precision is desired, we recommend increasing sample size, or developing models specific to the location or conditions of interest using the methodology of Vermeire and Gillen (2001).

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Sample numbers for microhistological estimation of fecal vizcacha diets

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Abstract

Precise estimates of diet composition are useful to assess herbivores impact on rangelands and to make management decisions. Since the variability within- and between-samples affect precision of estimates on diet studies, we studied this variability in diets of the rodent vizcacha (*Lagostomus maximus* Blainv.). We analyzed fecal pellets using a microhistological technique and we estimated the number of samples and subsamples required to achieve given confidence levels. Diets of this herbivore, which is thought to compete with cattle for forage, were studied in November 1994, May, July, and October 1995 in a mixed shrub-grassland community of the southern Caldenal in central Argentina. Most grasses, the main components of the diets (> 80%), were estimated with high precision (confidence interval: CI = 10%, $p = 0.05$) by observing 14 samples and 5 slides per sample. Forbs (5–6%) and shrubs (12%) were estimated with this same number of samples and slides, but yielded a lower level of precision (CI = 20%, $p = 0.10$). Although our results may not be directly applicable to other vegetation or herbivores, the procedures may be used in other situations to improve precision of diet estimates through microhistological analysis of feces.

Key Words: diet selection, precision, *Lagostomus maximus*, central Argentina, Caldenal.

When assessing food habits or effects of herbivores on the environment, it is important to obtain accurate measures of diet selection. The Sparks and Malechek (1968) technique has been frequently used to estimate diet botanical composition, although some factors affect its precision. Overestimation may arise from excessive fragmentation during slide preparation (Dearden et al. 1975), from a high ratio of identifiable/non-identifiable fragments (Havstad and Donart 1978), and from other factors that increase identification probability (Holechek and Gross 1982). Underestimation may also occur due to high digestibility of some taxa (Vavra and Holechek 1980, Holechek et al. 1982), due to low-identifiable/non-identifiable fragments ratio, and due to low degree of fragmentation during slide preparation.

One major factor to consider in diet studies is the number of

Resumen

Estimaciones precisas de la composición de dietas son útiles para determinar el impacto de los herbívoros en los pastizales naturales y tomar decisiones de manejo. Debido a que la variabilidad dentro de una muestra y entre muestras puede afectar la precisión de las estimaciones en los estudios de dieta, nosotros estudiamos esta variabilidad en las dietas del roedor vizcacha (*Lagostomus maximus* Blainv.). Analizamos pellets fecales empleando una técnica microhistológica y estimamos el número de muestras y submuestras requeridos para alcanzar determinados niveles de precisión. La dieta de estos herbívoros, que son considerados competidores de los vacunos por el forraje, se estudió en noviembre de 1994, mayo, julio y octubre de 1995 en una comunidad mixta de arbustal y pastizal en el sur del Caldenal en Argentina central. La mayoría de las gramíneas, componentes principales de las dietas (> 80%), fueron estimadas con alta precisión (intervalo de confianza: IC = 10%, $p = 0,05\%$) observando 14 muestras y 5 preparados por muestra. Las dicotiledóneas herbáceas anuales (5-6%) y arbustos (12%) fueron estimados con este mismo número de muestras y preparados pero alcanzando menor nivel de precisión (IC = 20%, $p = 0,10\%$). Si bien nuestros resultados no son directamente aplicables a otros tipos de vegetación o herbívoros, los procedimientos pueden ser usados en otras situaciones para mejorar la precisión en la estimación de dietas a través del análisis microhistológico de heces.

samples needed to obtain a desired level of precision for estimates. This has been studied with esophageal samples (Harniss et al. 1975, Brizuela et al. 1983) and with fecal samples (Bóo et al. 1991) from domestic livestock. Reports of such studies for wild herbivores were not detected. Variability in the estimation of diet components within samples will affect variability between samples. If low precision is achieved in within-sample mean estimates, low precision in the estimation of sample means may be expected, which in turn will increase the number of samples to estimate the population parameter for a given level of precision.

The objectives of this work were: 1) To study within- and between-sample variability on estimates of different components of vizcacha diets and 2) To calculate the number of samples per date and sub-samples per sample required for defined levels of precision when estimating vizcacha dietary composition.

Study area and methods

The study was conducted in a 600 ha pasture located in south-east La Pampa, Argentina (38°45'S, 63°45'W). Mean annual rain-

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fall is 448 mm with about 60% occurring in spring and fall. Rainfall during the study was 21.0 mm in November 1994, 2.8 mm in May 1995, 4.8 mm in July 1995, and 4.2 in October 1995. These values were below historical records for the same months (26, 16, 28, and 30 mm respectively). Due to this drought, annual forbs were scarce in the area (1.1–2.9% cover, Bontti et al. 1999) where they were usually abundant during wet springs.

Mean annual potential evapotranspiration is 800 mm (Peláez 1986), mean annual temperature is 15.3° C with a minimum mean of 7° C in July and a maximum mean of 23.6° C in January. Recorded maximum and minimum temperatures are 42.5° C and –12.8° C respectively.

Vegetation is characterized by woody species dominance and a rich herbaceous layer. Woody cover varies between 50 to 70% with caldén (*Prosopis caldenia* Burk.), algarrobo (*P. flexuosa* D. C.) and piquillín (*Condalia microphylla* Cav.) as the most abundant (Bóo and Peláez 1991). The herbaceous cover is 40–50% and is dominated by perennial cool season bunchgrasses such as flechilla negra (*Piptochaetium napostaense* (Speg.) Hack.) and flechilla fina (*Stipa tenuis* Phil.). Coirón (*S. speciosa* Trin. et Rupr.) and flechilla blanca (*S. gynerioides* Phil.) are abundant, and flechilla alta (*S. clarazii* Phil.), coirón-poa (*Poa ligularis* Nees), and cola de zorro (*Pappophorum mucronulatum* Nees) are less abundant (Bóo and Peláez 1991). Flechilla alta and coirón-poa, once abundant in pristine vegetation, were replaced by flechilla negra and flechilla fina under moderate continuous grazing (Distel and Bóo 1995). Bare ground (30–40 %) is colonized during wet years by annual forbs, mostly carretilla (*Medicago minima* (L.) Grufberg) and alfilerillo (*Erodium cicutarium* L'Herit, (Bóo and Peláez 1991)). Annual above ground net primary production in this plant community was 862 kg ha⁻¹, and 684 kg ha⁻¹ for flechilla fina and flechilla negra respectively in a year with 532 mm of rainfall (Distel and Fernández 1986, Distel 1987).

Twenty vizcacha colonies per date were sampled by collecting 1 group of fresh fecal pellets from each colony. Colonies were 200 to 500 m from one another and within the same pasture. The vegetation was homogeneous in the area under their influence. Further details regarding the study site are given by Bontti et al. (1999).

Fecal samples were dried at 60° C for 48 hours, ground through a 1 mm mesh, in preparation of microhistological analysis.

Modified Sparks and Malechek (1968) techniques were employed converting plant frequency in microscope fields to density. Hertwig's solution was not used and 40 fields per slide were observed. Each group of fecal pellets was considered a sample and microscopic slides from 1 sample were considered subsamples.

To study variability within a sample, 20 slides from a single sample per date were prepared and 40 microscope fields per slide were observed using 100X magnification for a total of 800 fields. To estimate variability between samples we used 20 samples per date with 5 slides per sample and 40 fields per slide generating a total of 200 fields per sample. Fragments were identified by comparing fecal material with a reference collection including all major species in the area (Lindström 1994, Lindström et al. 1998a, Lindström et al. 1998b).

The number of slides per sample and the number of samples for given confidence intervals were estimated using Snedecor's equation (1956):

$$n = t^2 CV^2/d^2 \quad (1)$$

where n is the number of samples, t is the tabulated Student's t value for a given error probability (in this study: p = 0.05 or

p = 0.10) and degrees of freedom of the sample, C.V. is the coefficient of variation and d is the half-width of the desired confidence interval expressed as a percent of the sample mean. In this study n was calculated using desired confidence intervals (CI) of 10 and 20 % of the mean. Arcsine transformation (degrees) of the mean percentage of each component was calculated prior to statistical analysis. This transformation is recommended when data expressed as percentages that lie outside the 30–70% range (Snedecor and Cochran 1980).

Results and Discussion

Variability within samples

Grasses were main contributors to the diets throughout the study (Tables 1 and 2). Considering all sampling dates, high precision (CI = 10%, p = 0.05) in the estimation of flechilla negra and flechilla fina could be achieved by observing up to 3 slides (Table 1). Three to 9 slides were needed to obtain best estimates (CI = 10%, p = 0.05) of coirón. Analyzing 7 to 9 slides per sample would be very time consuming, especially when a high number of samples must be quantified (i.e. monthly).

Table 1. Mean percentage ($\bar{x}$) of major vizcacha diet components¹ describing within- sample variation; coefficients of variation, and number of subsamples (rounded values) required for 95 and 90% probability levels (p), and 10 and 20% confidence intervals (CI) in central Argentina from 1994 to 1995.

Date and species	$\bar{x}$	C.V.	Number of subsamples			
			p = 0.05		p = 0.10	
			10% CI	20% CI	10% CI	20% CI
November 1994	(%)		(No.)			
Grasses						
Flechilla negra	67.8	4.4	1	1	1	1
Flechilla fina	9.5	6.0	2	1	2	1
Coirón	5.4	7.1	3	1	2	1
Forbs						
Alfilerillo	5.1	8.5	4	1	3	1
Carretilla	4.7	9.6	5	1	3	1
May 1995						
Grasses						
Flechilla negra	62.1	8.6	2	1	2	1
Flechilla fina	27.1	12.7	3	1	2	1
July 1995						
Grasses						
Flechilla negra	52.4	6.9	1	1	1	1
Flechilla fina	19.6	13	3	1	2	1
Coirón	10.6	26.6	9	3	6	2
Shrubs						
Piquillín	12.1	24.7	8	2	5	2
October 1995						
Grasses						
Flechilla negra	49.3	8.4	2	1	1	1
Flechilla fina	19.8	16.8	4	1	3	1
Coirón	17.8	22.5	7	2	5	2

¹ Plant species contributing < 4% of the total diet were excluded.

Thus, it would be possible to estimate the contribution of coirón with 3 slides in July and with 2 slides in October, but with a lower level of precision (CI = 20%, $p = 0.05$) in both months.

Only low amounts of 2 forbs, carretilla and alfilerillo were detected in fecal samples in November 1994 (Table 1). Both could be estimated with high levels of precision (CI = 10%, $p = 0.05$) by observing 5 slides. Even though forbs are usually underestimated by fecal microhistological analysis, they were very scarce in the field due to the drought, and we believe that consumption was low. In the case of carretilla, most of the material on the ground were pods from the previous growing season.

Piquillín was the only woody species found in vizcacha diets. Again, the high number of slides necessary to achieve a high level of precision (CI = 10%, $p = 0.05$) for this species would be too time consuming, but an acceptable level of precision (CI = 20%, $p = 0.05$) could be achieved analyzing 2 slides (Table 1).

Considering all sampling dates and species, ≤ 5 slides would be adequate to estimate some species (i.e. flechilla negra, flechilla fina, alfilerillo and carretilla) with good precision (CI = 10%, $p = 0.05$), whereas ≤ 5 slides for other species with small contribution to the diets such as coirón and piquillín would be adequate for a lower level of precision (CI = 20%, $p = 0.05$).

Variability between samples

Flechilla negra and flechilla fina were the bulk of vizcacha diets throughout the study (Table 2). Considering all dates, these species can be estimated with the highest precision (CI = 10%, $p = 0.05$) analyzing ≤ 6 samples. Ten samples would be necessary to obtain the same precision with coirón (in October), a grass that was consistently less abundant in the diets for all dates.

Forbs (i.e. alfilerillo and carretilla) were detected only in low percentages in November 1994 and October 1995 (Table 2). Analyzing 18 samples provided a good estimation (CI = 10%, $p = 0.05$) in November and a less precise estimation (CI = 20%, $p = 0.05$) in October. The analysis of 12 samples would yield the lowest precision (CI = 20%, $p = 0.10$), but this could be an acceptable estimate considering the low contribution of forbs (5 and 6 %) to vizcacha diets.

Piquillín, the only woody species present in the diets (Table 2, July), showed high variability (CV = 70%). Twenty samples would give an estimate within 20% of the mean ($p = 0.05$), but this number

would be too costly for long-term studies.

The number of samples analyzed in a long-term study depends on inherent variability of the samples, the objective of the study, and available resources. Considering that resources are usually limiting, analyzing 14 samples per date would give precise estimation (CI = 10%, $p = 0.05$) of the major components (i.e. grasses). However, minor components such as forbs and woody species would be estimated with low precision. In our experience, a trained operator would need about 90 minutes to process 5 slides from 1 sample while observing 40 fields per slide (\$7.5 labor, \$2.5 materials).

Considering between samples analysis, precision in this work was higher than reported in studies by Harniss et al. (1975) and Brizuela et al. (1983). This may be due to 2 reasons. First, the cited studies used fistulated animals which restricted the number of available samples and expanded confidence intervals and second, 40 microscope fields per slide were observed in this study as compared to 20 observed fields in the studies mentioned above. A larger number of observations may contribute to smaller variances and coefficients of variation but would also increase the cost of the analysis.

Comparison of variability within- and between samples

As expected, low number of samples gives precise estimates for species with low within- between-sample coefficients of variation (Tables 1 and 2). In general, major increases in sample size occurred when dietary components were below 10% (Tables 1 and 2).

Even though in November 1994 the within-sample coefficient of variation for forbs was slightly higher than for grasses, the between-sample coefficient of variation for alfilerillo was dramatically higher than for grasses. This suggests that high digestibility, characteristic of many forbs, may cause underestimation of alfilerillo in microhistological analyses of fecal samples (Vavra and Holechek 1980, Holechek et al. 1982). In addition, when forbs are scarce in the ingesta, high digestibility could cause disappearance or errors in the detection of fragments and a consequent increase in the sample variance.

A different situation may have occurred with carretilla, where the leaves have structures (i.e. calcium oxalate crystals) that allow easy identification (Lindström 1994). However, due to the pronounced drought during the study, most of the carretilla consumed by vizcachas were fruits

Table 2. Mean percentage ($\bar{x}$) of major vizcacha diet components¹ describing between-sample variation; coefficients of variation, and number of colonies sampled (rounded values) required for 95 or 90% probability levels (p), and 10 and 20% confidence intervals (CI) in central Argentina from 1994 to 1995.

Date and species	$\bar{x}$	C.V.	Number of colonies			
			$p = 0.05$		$p = 0.10$	
			10% CI	20% CI	10% CI	20% CI
November 1994	(%)		(No.)			
<u>Grasses</u>						
Flechilla negra	69.4	3.	1	1	1	1
Flechilla fina	10.3	8.0	1	1	1	1
Coirón	4.9	27.0	5	2	4	1
<u>Forbs</u>						
Alfilerillo	6.0	47.0	18	5	13	3
May 1995						
<u>Grasses</u>						
Flechilla negra	70.2	22	2	1	2	1
Flechilla fina	23.4	27	4	1	3	1
July 1995						
<u>Grasses</u>						
Flechilla negra	44.9	22	5	1	3	1
Flechilla fina	22.3	20	5	2	3	1
Coirón	12.1	32	7	2	5	2
<u>Shrubs</u>						
Piquillín	12.2	70	77	20	53	14
October 1995						
<u>Grasses</u>						
Flechilla negra	44.3	22	5	2	3	1
Flechilla fina	24.9	23	6	2	5	1
Coirón	15.3	31	10	3	7	2
<u>Forbs</u>						
Carretilla	5.0	95	71	18	49	12

¹Plant species contributing < 4% of the total diet were excluded

or parts of fruits from the previous growing cycle. These materials were difficult to identify and this could partially explain the high CV that we found in October 1995 (Table 2).

In July 1995 the within-sample coefficient of variation for piquillín was similar to coirón (Table 1), but the between-sample coefficient of variation for the shrub was twice higher than for coirón (Table 2). Piquillín, in spite of being abundant in the field, only appeared in diets when forage resources were very scarce (Bontti et al. 1999). Consumption of piquillín by some animals was often erratic, causing a high sample variance. Shrubs are difficult to estimate when a high stem/leaf proportion is present in the diet (Holechek and Valdez 1985) and this can also explain the high between-sample variance. These results indicate that microhistological analysis of feces may be most appropriate when the bulk of the diets are grasses rather than forbs or shrubs.

Our results indicate that this procedure may be adapted for specific vegetation and herbivore type in other studies. This methodology could also be used to evaluate the technique at different phenological types or when the plant community changes in response to specific climatic conditions. For example, annual forbs consumption may be difficult to determine because of their high digestibility, but their abundance in the plant community usually depends on average or above average rains during the spring. When such situations occur, additional samples may be collected at specific sampling dates to estimate forbs with a desired level of precision.

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Vegetation of prairie dog colonies and non-colonized short-grass prairie

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Abstract

Black-tailed prairie dogs have declined by 98% in the past century. Due to continued declines, the U. S. Fish and Wildlife Service designated the species as a candidate for listing in 2000. Prairie dogs foster both plant and animal diversity, and their continued presence is a concern in the Great Plains. We compared vegetation structure and composition of black-tailed prairie dog (*Cynomys ludovicianus* Ord) colonies in southwest Kansas and southeast Colorado to non-colonized grassland in 1996, and 1997. Dominant species on prairie dog colonies were *Bouteloua gracilis* (H. B. K.) Lag. ex Griffiths (14% cover in 1996, 15% in 1997), *Buchloe dactyloides* (Nutt.) Engelm. (7% cover in 1996, 17% in 1997) and *Aristida purpurea* Nutt. (9% cover in 1996, 16% in 1997). Dominant vegetation at randomly selected non-colonized sites were *Bouteloua curtipendula* (Michx.) Torr. (16% cover in 1996, 18% in 1997), *Bouteloua gracilis* (13% cover in 1996, 17% in 1997) and *Buchloe dactyloides* (5% cover in 1996, 5% in 1997). Non-colonized shortgrass sites were dominated by *Bouteloua gracilis* (23% cover in 1996, 41% in 1997) and *Buchloe dactyloides* (8% cover in 1996, 12% in 1997). Cover of grass was higher ($P < 0.01$) on random sites (44%) than on prairie dog colonies (31%) or shortgrass sites (33%) in 1996, whereas cover of forbs was higher ($P < 0.01$) on prairie dog colonies (18%) than on random sites (7%) or shortgrass sites (8%) that year. Vegetation height was greater ($Q = 3.66$) and visual obstruction was greater ($Q = 3.39$) on random sites (33.6 and 6.4 cm, respectively) than on prairie dog colonies (9.5 and 2.5 cm, respectively) in 1997, the only year these variables were measured. Percent bare ground did not differ ($P > 0.05$) among treatments either year. While components of the vegetation on prairie dog colonies differed from that found on non-colonized sites, the vegetation of prairie dog colonies was, nonetheless, characteristic of a shortgrass region. Prairie dogs undoubtedly alter vegetation structure and composition in shortgrass prairie, and likely have a great influence on landscape heterogeneity, but our results suggest that shortgrass prairie is well adapted to the herbivory and soil disturbing activities of prairie dogs.

Resumen

La población del perro de la pradera (cola negra) (*Cynomys ludovicianus* Ord) ha disminuido por 98% durante el siglo pasado. Debido a la reducción de su población, el perro de la pradera fue designado por el U.S. Fish and Wildlife Service (Servicio Estadounidense de Pesca y Vida Silvestre) con un estatus de candidato, en peligro de extinción. Los biólogos se preocupan por la existencia continuada del perro de la pradera porque esta especie fomenta la biodiversidad en los ecosistemas donde habita. En la presente investigación, comparamos la estructura y composición del la vegetación de praderas colonizadas y no-colonizadas por perros de la pradera, en el suroeste de Kansas y el sureste de Colorado, en 1996 y 1997. Las especies dominantes en las colonias de perros de la pradera eran *Bouteloua gracilis* (H.B.K.) Lag ex Griffiths (14% y 15% cobertura en 1996 y 1997, respectivamente), *Buchloe dactyloides* (Nutt.) Engelm. (7% y 17% cobertura en 1996 y 1997, respectivamente) y *Aristida purpurea* (9% y 16% cobertura en 1996 y 1997, respectivamente). La cobertura de vegetación dominante en sitios no-colonizados por perros de la pradera, seleccionados al azar, era *Bouteloua curtipendula* (Michx.) Torr. (16% y 18% en 1996 y 1997), *Bouteloua gracilis* (13% y 17% en 1996 y 1997) y *Buchloe dactyloides* (5% en ambos años). En las praderas bajas no-colonizadas por perros de la pradera, las plantas predominantes eran *Bouteloua gracilis* (23% y 41% cobertura en 1996 y 1997) y *Buchloe dactyloides* (8% y 12% cobertura en 1996 y 1997). La cobertura de gramíneas era mayor ($P < 0.01$) en los sitios seleccionados al azar (44%) que en las colonias de perros de la pradera (31%) o praderas bajas (33%) en 1996. Al contrario, la cobertura de plantas herbáceas era mayor ($P < 0.01$) en las colonias de perros de la pradera (18%) que en los sitios seleccionados al azar (7%) o en las praderas bajas (8%) durante el mismo año. La altura de vegetación era mayor ($Q = 3.66$) y la obstrucción visual era mayor ($Q = 3.39$) en los sitios seleccionados al azar (33.6 y 6.4 cm, respectivamente) que en las colonias de perros de la pradera (9.5 y 2.5 cm, respectivamente) en 1997, el único año que estos datos eran medidos. No existía diferencias ($P > 0.05$) en el porcentaje de suelo abierto entre los tratamientos durante ambos años. Aunque existen diferencias en algunos componentes de la vegetación de las colonias de perros de la pradera y los sitios no-colonizados, sin embargo la vegetación de las colonias era característica de la región de praderas bajas. Los perros de la pradera ciertamente alteran la estructura y composición de la pradera baja, y probablemente tienen gran influencia sobre la heterogeneidad del paisaje. No obstante, los resultados sugieren que la pradera baja está bien adaptada al herbívoro y los estorbos edáficos de los perros de la pradera.

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Key Words: black-tailed prairie dog, *Cynomys ludovicianus*, cover, bare ground, frequency, shortgrass prairie, herbivory, soil disturbance

Black-tailed prairie dogs (*Cynomys ludovicianus* Ord) alter vegetation structure, composition, and ecosystem dynamics in South Dakota mixed-grass prairie (Agnew et al. 1986, Archer et al. 1987, Cid et al. 1991, Coppock et al. 1983, Krueger 1986), Texas mixed-grass prairie (Weltzin et al. 1997b), Texas mesquite (*Prosopis glandulosa* Torr.) savanna (Weltzin et al. 1997a), and Colorado shortgrass prairie (Bonham and Lerwick 1976). The importance of prairie dog ecosystems to numerous vertebrates in the Great Plains has been demonstrated (Kotliar et al. 1999), and increased awareness of this role has prompted appeals for heightened protection of prairie dogs and changes to the management of public and private rangelands (Miller et al. 1994, Davitt et al. 1996). Black-tailed prairie dogs have declined by 98% in the past century, and due to continued recent declines, the U.S. Fish and Wildlife Service designated the species as a candidate for listing in 2000 (U.S.D.I. 2000).

The states across the range of black-tailed prairie dogs are developing an interstate conservation strategy for the species, so prairie dog conservation efforts will increasingly influence future management of western rangelands (Van Pelt 2000). Accurate information on the effects of prairie dogs on vegetation in different areas of their range will contribute significantly to rangeland management. Our purpose was to quantify differences in vegetation among prairie dog colonies and non-colonized sites in the shortgrass prairie of southwest Kansas and southeast Colorado. These findings will enhance prairie dog conservation as well as cooperation of land managers, livestock producers, conservationists, and policy makers in ensuring the maintenance of biotic integrity and economic vitality of western rangelands.

Study Sites and Methods

Study sites were located at Cimarron National Grassland in Morton County, southwest Kansas, and adjacent private lands in Baca County, southeast Colorado (lat 37° 07'N, Long. 102° 00'W). Cimarron National Grassland comprises > 43,700 ha of predominantly grazed land administered by the U.S. Forest Service. Most of the surrounding private land is cropped,

but some areas remain in perennial grass cover and are grazed by cattle (*Bos taurus* L.). A substantial portion of Cimarron National Grassland is abandoned farmland that was reclaimed between 1930 and 1950 in the Morton County Land Utilization Project (Schumacher and Atkins 1965), and it is unlikely that any of our study sites represent undisturbed relict vegetation (T. Watson, USDA-NRCS, pers. comm.).

Many areas at Cimarron National Grassland are characterized by mid-height vegetation, which may reflect the composition of seed mixes used to reclaim abandoned farmland in the 1930's to 1950's (Schumacher and Atkins 1965). Other areas are characterized by shorter vegetation which may reflect past grazing history. We chose to compare the vegetation on prairie dog colonies to 2 types of non-colonized grassland: 1) areas of short vegetation that are presumably characteristic of a shortgrass region (shortgrass sites), and 2) randomly selected areas (random sites). The criterion used to select shortgrass sites was a visual determination of dominance by the perennial shortgrasses *Buchloe dactyloides* (Nutt.) Engelm. and *Bouteloua gracilis* (H. B. K.) Lag. ex Griffiths. Conversely, random sites were selected from a list of potential sites that had soil types and slopes identical to those characterizing the prairie dog colonies. Selection of random sites occurred without knowledge of the vegetation present at those sites.

All study sites occupied upland range sites characterized by loamy and silty loam soils within the Richfield-Ulysses association, with slopes between 0 to 6% (Dickey et al. 1963). Even though soil type was not considered in the selection of shortgrass sites, soil type and slope of these sites were identical to those of prairie dog colonies. Mean precipitation (1901–1996) at the Elkhart weather station in Morton County is 44.8 cm (National Weather Service Cooperative Observer Network, Pers. Comm.). Precipitation during the 12 months prior to sampling in 1996 (1 July 1995, to 30 June 1996) was 34.3 cm, 76 % of the long term mean. Precipitation during the 12 months prior to sampling in 1997 (1 July 1996, to 30 June 1997) was 68.0 cm, 152% of the long term mean.

In 1996 we selected 8 of the largest prairie dog colonies on Cimarron National Grassland ($\bar{x}$ = 41.49 ha, range = 20–64 ha, total approximately 332 ha) for sampling. For comparison we selected 8 random sites ($\bar{x}$ = 56.68 ha, range = 32–64 ha, total approximately 454 ha) and 5 non-col-

onized shortgrass sites on Cimarron National Grassland ($\bar{x}$ = 42.10 ha, range = 32–64 ha, total approximately 210 ha). Between the 1996 and 1997 field seasons, one of the prairie dog colonies had been destroyed by plague (Cully et al. 2000) and the boundaries of another changed sufficiently to make it unsuitable for sampling, so these sites were not sampled in 1997. Completion of the 1996 field season indicated that it would be logistically possible to sample more sites, so 7 additional prairie dog colonies on Cimarron National Grassland and adjacent private lands were sampled in 1997 (n = 13, $\bar{x}$ = 39.25 ha, range = 8–125 ha, total approximately 555 ha) as well as 1 additional shortgrass site on private land (n = 6, $\bar{x}$ = 43.18 ha, range = 32–64 ha, total approximately 260 ha). The 8 random sites evaluated in 1996 were sampled again in 1997. The exact age of prairie dog colonies sampled in this study is unknown, but at least 6 of the colonies were present in 1989 (Behan 1989).

Cattle grazing occurred at all sites prior to the study, with periods of use being variable. Season-long, rotational grazing, and fall and winter grazing were all practiced on Cimarron National Grassland and adjacent private lands. Three prairie dog colonies and 2 shortgrass sites were not grazed by cattle in 1996 and 1997. Due to drought conditions in 1996, cattle turnout did not occur until 17 June. In 1997, cattle turnout occurred as early as 1 May. Determination of exact grazing dates and AUM's for each study site from Forest Service grazing schedules was not possible because permittees did not rigorously adhere to grazing plans. Also, such data would have questionable value because stock were not uniformly distributed about the area.

In 1996, sampling occurred between 1 July and 18 July. In 1997, sampling occurred between 18 June and 2 July. Sampling was conducted using a 10.0-m² circular plot centered on one corner of a 0.10-m² rectangular plot. Canopy cover of grass, forbs, canopy cover of individual species, and percent bare ground were estimated within the 0.10-m² plot. Frequency of occurrence of each species was quantified using both the 0.10-m² and the 10.0-m² plot. The appropriate plot size for detecting statistical differences in the frequency of a species is influenced by the density and dispersion of that species within a community (Hyder et al. 1963, 1965, 1975). Previous research in shortgrass prairie has shown that small plots sample the dominant grass, *Bouteloua gracilis*, at optimal frequencies, but fail to

detect less common species (Hyder et al. 1965, 1975). We used 2 different plot sizes because concurrent use of small and large plots insures adequate sampling of species which are common and abundant, as well as species which are less commonly encountered (Hyder et al. 1965, 1975).

Congeneric species that were difficult to differentiate in the field, such as *Amaranthus albus* L., *A. graecizans* L., *A. palmeri* S. Wats. and *A. retroflexus* L., were grouped into single taxonomic groups for data analysis (e.g. *Amaranthus* spp). Nomenclature follows Great Plains Flora Association (1986). In 1996, sampling occurred at 40 randomly located points at each study site. To facilitate the sampling of small prairie dog colonies in 1997, the number of randomly located points sampled at each site was proportional to the area of the site, thus only 20 points were sampled at some of the smaller prairie dog colonies while up to 60 points were sampled at some of the larger random sites.

In 1997, between 27 May and 18 June, vegetation structure was measured using a visual obstruction pole modified from Robel et al. (1970) at randomly located points along transects at each study site. Again, number of points sampled at each site varied from 35 to 120 in proportion to the area of the site. The visual obstruction pole was marked in 1 cm increments, and observations were made 1 meter from the pole at a height of 1 meter. One observation was made from each of the 4 cardinal directions at each point, and a mean calculated for each point. Vegetation height was determined by recording the highest point at which vegetation crossed between the observer and the pole. Visual obstruction was determined by recording the lowest point at which the pole was visible.

Species richness, Shannon's diversity index (H'), an evenness measure based on Shannon's diversity index (E), and the inverse of Simpson's diversity index ($1/D$) were calculated using frequency data from both the 0.10-m² and the 10.0-m² plots. Diversity index equations were obtained from Magurran (1988). Lower values for H' , E and $1/D$ indicate lower diversity, or a less equitable distribution of abundances among species in a sample, whereas higher values indicate more species or that abundances among species are more equitably distributed (Magurran 1988). Extreme dominance by 1 or a few species in a sample can reduce values of H' , E , and $1/D$, whereas maximum values are obtained when all species have equal abundances (Magurran 1988). Species

richness and diversity indices for 1996 were calculated by determining the total number of species encountered at each study site (40 plots sampled per site). Because the number of points sampled at each site was variable in 1997, richness and diversity values generated using all plots at each site would not be comparable among treatments. Richness and diversity indices for 1997 were calculated by determining the number of species encountered on a 10-plot basis at each study site. Plots within each study replicate were assigned to 10 plot groups on a random basis without replacement. Richness and diversity indices for each study site were then obtained by calculating the mean of the 10-plot groups within each site.

Two-tailed tests were used to test the null hypothesis that there was not a significant difference among the means of the 3 treatments (prairie dog colonies, random sites, and shortgrass sites). The experimental units were each site within a treatment (i.e. 8 prairie dog colonies in 1996, 13 in 1997). Response variables were % cover, % bare ground, vegetation height, visual obstruction, and frequency. Data from the 2 years were not combined for analysis because of the different sampling times in each year and the addition and deletion of study sites between the 2 years. For statistical analysis we used one-factor ANOVA with 3 treatments, using SAS v. 6.11 proc glm (1996), when the assumptions of the F-test were satisfied. When the

assumptions of the F-test were not satisfied, we used the Kruskal-Wallis non-parametric test (SAS v. 6.11 proc npar1way 1996) and a Tukey-type non-parametric multiple comparison method (Zar 1996). We set $\alpha = 0.05$ for hypothesis tests. A test statistic value of $Q > 2.39$ generated by the Tukey-type test indicated significant differences. When a species was detected at only 1 site it was not included in statistical evaluations.

Results

In 1996 and 1997, respectively, we detected a total of 84 and 92 plant species or taxonomic groups on prairie dog colonies, 91 and 96 on random sites, and 75 and 87 on shortgrass sites. During the 2 years, 6 species and 2 taxonomic groups were restricted to prairie dog colonies and 23 species were restricted to non-colonized sites. Nine of the 23 were encountered only on random sites, while 7 were encountered only on shortgrass sites. When frequency data from both the 0.10-m² and 10.0-m² plots were used to calculate species richness and diversity indices in 1996 and 1997, there were no significant differences ($P > 0.05$) among any of the treatments (Table 1).

In 1996, more grass cover ($P < 0.01$) occurred on random sites than on prairie dog colonies or shortgrass sites, while grass cover was similar among treatments

Table 1. Mean ($\pm$ SE) species richness, Shannon's diversity index (H'), an evenness measure based on Shannon's diversity index (E) and the inverse of Simpson's diversity index ($1/D$) of vegetation sampled in prairie dog colonies, non-colonized random sites and non-colonized shortgrass sites during 1996 ($n = 8, 8$, and 5 , respectively), and 1997 ($n = 13, 8$, and 6 , respectively), in Kansas and Colorado.

	Prairie Dog Colonies	Random Sites	Shortgrass Sites
0.10-m ² plots - 1996			
richness	20.25 $\pm$ 1.05	18.13 $\pm$ 1.83	18.60 $\pm$ 2.52
H'	2.36 $\pm$ 0.05	2.20 $\pm$ 0.13	2.20 $\pm$ 0.17
E	0.79 $\pm$ 0.02	0.77 $\pm$ 0.02	0.76 $\pm$ 0.02
$1/D$	8.06 $\pm$ 0.50	7.21 $\pm$ 1.04	7.14 $\pm$ 1.41
10.0-m ² plots - 1996			
richness	41.38 $\pm$ 2.28	44.63 $\pm$ 1.99	41.2 $\pm$ 2.08
H'	3.18 $\pm$ 0.05	3.21 $\pm$ 0.07	3.12 $\pm$ 0.04
E	0.86 $\pm$ 0.01	0.85 $\pm$ 0.01	0.84 $\pm$ 0.01
$1/D$	19.91 $\pm$ 0.81	19.68 $\pm$ 1.75	18.37 $\pm$ 1.06
0.10-m ² plots - 1997			
richness	11.31 $\pm$ 0.89	11.00 $\pm$ 0.77	11.25 $\pm$ 1.06
H'	2.05 $\pm$ 0.09	2.07 $\pm$ 0.09	2.09 $\pm$ 0.11
E	0.86 $\pm$ 0.01	0.88 $\pm$ 0.01	0.88 $\pm$ 0.01
$1/D$	8.11 $\pm$ 0.87	8.74 $\pm$ 0.87	8.88 $\pm$ 1.69
10.0-m ² plots - 1997			
richness	29.21 $\pm$ 1.32	29.94 $\pm$ 1.53	28.06 $\pm$ 1.37
H'	3.05 $\pm$ 0.06	3.09 $\pm$ 0.06	3.01 $\pm$ 0.06
E	0.91 $\pm$ 0.01	0.91 $\pm$ 0.01	0.91 $\pm$ 0.01
$1/D$	21.15 $\pm$ 1.34	22.37 $\pm$ 1.44	20.16 $\pm$ 1.53

Table 2. Mean cover ($\pm$ SE) of grasses, forbs, bare ground and the 4 dominant grasses on prairie dog colonies, non-colonized random sites and non-colonized shortgrass sites in 1996 (n = 8, 8 and 5, respectively) and 1997 (n = 13, 8, and 6, respectively), and mean ($\pm$ SE) vegetation height and visual obstruction in 1997, in Kansas and Colorado. Different superscripts within rows indicate significant differences ($P < 0.05$ or $Q > 2.39$) from pair-wise comparisons.

	Prairie Dog Colonies	Random Sites	Shortgrass Sites
1996			
grass	30.71 $\pm$ 1.79 ^a	44.29 $\pm$ 2.19 ^b	32.84 $\pm$ 1.23 ^a
forb	18.31 $\pm$ 2.96 ^a	7.11 $\pm$ 1.73 ^b	7.63 $\pm$ 1.47 ^b
bare ground	30.11 $\pm$ 3.17 ^a	32.10 $\pm$ 3.08 ^a	28.25 $\pm$ 1.95 ^a
<i>Aristida purpurea</i> Nutt.	8.53 $\pm$ 1.86 ^a	4.29 $\pm$ 1.62 ^{ab}	1.67 $\pm$ 0.47 ^b
<i>Bouteloua curtipendula</i> (Michx.) Torr.	0.13 $\pm$ 0.12 ^a	16.38 $\pm$ 4.64 ^b	0.09 $\pm$ 0.07 ^a
<i>Bouteloua gracilis</i> (H. B. K.) Lag. ex Griffiths	14.28 $\pm$ 4.60 ^a	13.18 $\pm$ 2.69 ^a	22.99 $\pm$ 3.08 ^a
<i>Buchloe dactyloides</i> (Nutt.) Engelm.	7.16 $\pm$ 1.53 ^a	5.08 $\pm$ 2.98 ^a	7.62 $\pm$ 1.74 ^a
1997			
grass	51.85 $\pm$ 3.10 ^a	51.41 $\pm$ 0.68 ^a	60.01 $\pm$ 2.90 ^a
forb	10.56 $\pm$ 2.57 ^a	10.01 $\pm$ 1.96 ^a	6.37 $\pm$ 1.39 ^a
bare ground	32.70 $\pm$ 2.61 ^a	32.38 $\pm$ 1.55 ^a	27.06 $\pm$ 4.54 ^a
<i>Aristida purpurea</i> Nutt.	15.60 $\pm$ 2.74 ^a	4.92 $\pm$ 1.30 ^{ab}	4.12 $\pm$ 0.88 ^b
<i>Bouteloua curtipendula</i> (Michx.) Torr.	0.06 $\pm$ 0.06 ^a	17.85 $\pm$ 5.37 ^b	2.67 $\pm$ 1.39 ^{ab}
<i>Bouteloua gracilis</i> (H. B. K.) Lag. ex Griffiths	15.07 $\pm$ 4.70 ^a	16.74 $\pm$ 3.02 ^a	40.80 $\pm$ 6.61 ^b
<i>Buchloe dactyloides</i> (Nutt.) Engelm.	17.44 $\pm$ 4.68 ^a	5.12 $\pm$ 2.51 ^a	12.29 $\pm$ 3.61 ^a
vegetation height	9.48 $\pm$ 0.80 ^a	33.59 $\pm$ 3.29 ^b	25.22 $\pm$ 5.50 ^{ab}
visual obstruction	2.49 $\pm$ 0.17 ^a	6.41 $\pm$ 1.32 ^b	5.40 $\pm$ 1.22 ^{ab}

in 1997 (Table 2). In 1996, more forb cover ($P < 0.01$) occurred on prairie dog colonies than on random or shortgrass sites, but was similar ($P > 0.05$) among treatments in 1997. The amount of bare ground was similar ($P > 0.05$) among treatments in 1996 and 1997. In 1997, vegetation height was greater ($Q = 3.66$) and visual obstruction was greater ($Q = 3.39$) on random sites than on prairie dog colonies.

Based on cover, the 4 most dominant grasses were *Aristida purpurea* Nutt., *Bouteloua curtipendula* (Michx.) Torr., *Bouteloua gracilis* and *Buchloe dactyloides*. In 1996, there was more cover of *Bouteloua curtipendula* on random sites than on prairie dog colonies ($Q = 3.11$) or shortgrass sites ($Q = 2.47$), and there was more ($P = 0.01$) cover of *Aristida purpurea* on prairie dog colonies than on shortgrass sites (Table 2). In 1997, there was more cover of *Bouteloua gracilis* on shortgrass sites than on the prairie dog colonies ($P < 0.01$) or the random sites ($P < 0.01$), more ($Q = 3.84$) cover of *Bouteloua curtipendula* on the random sites than on the prairie dog colonies, and more ($Q = 2.92$) cover of *Aristida purpurea* on the prairie dog colonies than on the shortgrass sites.

Across years and plot sizes, 7 species or taxonomic groups of perennial forbs were more frequent on random sites than on prairie dog colonies during at least 1 year (Tables 3 and 4). Using the 0.10-m² plot, this difference was detected for *Psoralea tenuifolia* Pursh in 1997 ($P < 0.01$). Using the 10.0-m² plot, this difference was

detected for *Astragalus lotiflorus* Hook. in 1996 ($P = 0.04$), *Gaura coccinea* Pursh in 1997 ($P < 0.01$), *Asclepias latifolia* (Torr.) Raf. in 1997 ($Q = 2.78$), *Convolvulus equitans* Benth. in 1997 ($Q = 3.49$), *Thelesperma* spp. in 1997 ($Q = 3.32$) and *Trapopogon dubius* Scop. in 1997 ($Q = 3.07$). There were no perennial forbs more frequent on prairie dog colonies than random sites.

Across years and plot sizes, 5 species or taxonomic groups of annual forbs were more frequent on prairie dog colonies than on random sites (Tables 3 and 4). Using the 0.10-m² plot, this difference was detected for *Amaranthus* spp. ($P = 0.01$) and *Euphorbia* spp. ($P < 0.01$) in 1996.

Table 3. Mean frequencies ($\pm$ SE) of species that differed significantly among treatments during sampling of prairie dog colonies, non-colonized random sites and non-colonized shortgrass sites (n = 8, 8, and 5, respectively) in Kansas and Colorado during 1996. Different superscripts within rows indicate significant differences ($P < 0.05$ or $Q > 2.39$) from pair-wise comparisons.

	Prairie Dog Colonies	Random Sites	Shortgrass Sites
0.10-m ² plots			
<i>Amaranthus</i> spp. ¹	0.09 $\pm$ 0.04 ^a	0.01 $\pm$ 0.01 ^b	0
<i>Euphorbia</i> spp. ²	0.72 $\pm$ 0.07 ^a	0.23 $\pm$ 0.09 ^b	0.56 $\pm$ 0.09 ^a
<i>Aristida purpurea</i> Nutt.	0.55 $\pm$ 0.09 ^a	0.28 $\pm$ 0.08 ^b	0.16 $\pm$ 0.04 ^b
<i>Bouteloua curtipendula</i> (Michx.) Torr.	0.01 $\pm$ 0.01 ^a	0.46 $\pm$ 0.12 ^b	0.01 $\pm$ 0.01 ^a
<i>Bouteloua gracilis</i> (H. B. K.) Lag. ex Griffiths	0.54 $\pm$ 0.12 ^a	0.41 $\pm$ 0.08 ^a	0.89 $\pm$ 0.05 ^b
10.0-m ² plots			
<i>Astragalus lotiflorus</i> Hook.	0.02 $\pm$ 0.01 ^a	0.11 $\pm$ 0.04 ^b	0
<i>Euphorbia</i> spp. ²	0.93 $\pm$ 0.03 ^a	0.50 $\pm$ 0.12 ^b	0.93 $\pm$ 0.05 ^{ab}
<i>Cryptantha minima</i> Rydb.	0.01 $\pm$ 0.01	0	0
<i>Ambrosia confertifolia</i> DC.	0.05 $\pm$ 0.03 ^{ab}	0.01 $\pm$ 0.01 ^a	0.11 $\pm$ 0.06 ^b
<i>Bouteloua curtipendula</i> (Michx.) Torr.	0.01 $\pm$ 0.01 ^a	0.62 $\pm$ 0.14 ^b	0.04 $\pm$ 0.02 ^{ab}
<i>Buchloe dactyloides</i> (Nutt.) Engelm.	0.68 $\pm$ 0.07 ^{ab}	0.39 $\pm$ 0.14 ^a	0.88 $\pm$ 0.05 ^b

¹*Amaranthus albus* L., *A. graecizans* L., *A. palmeri* S. Wats., and *A. retroflexus* L.

²*Euphorbia glyptosperma* Engelm., *E. missurica* Raf., and *E. serpyllifolia* Pers.

Using the 10.0-m² plot, this difference was detected for *Kochia scoparia* (L.) Schrad. ($Q = 3.33$), *Salsola* spp. in 1997 ($P < 0.01$), *Euphorbia strictospora* Engelm. in 1997 ($Q = 3.15$), and for *Euphorbia* spp. in 1996 ($P < 0.01$). In both years, the annual forb, *Cryptantha minima* Rydb., was only detected on prairie dog colonies. There were no annual forbs more frequent on random sites than prairie dog colonies.

Use of the 0.10-m² plot indicated the annual grass *Hordeum pusillum* Nutt. was more frequent ($P < 0.01$) on shortgrass sites than prairie dog colonies in 1997 (Table 4). Another annual grass, *Bromus japonicus* Thunb. ex Murr., was not detected on prairie dog colonies during either year, but occurred on random and shortgrass sites in 1997. Frequencies of all other annual grasses were similar ($P > 0.05$) when prairie dog colonies were compared to shortgrass sites and random sites.

Higher frequencies ($P \leq 0.02$ in 1996, $Q \geq 2.68$ in 1997) of the perennial grass *Aristida purpurea* on prairie dog colonies than random and shortgrass sites were detected when the 0.10-m² plot was used, while both plot sizes indicated the perennial grass *Schedonnardus paniculatus* was more frequent ($P \leq 0.01$) on prairie dog colonies than random and shortgrass sites in 1997. Use of the 10.0-m² plot in 1997 indicated the perennial grass *Buchloe dactyloides* was more frequent ($P = 0.01$) on prairie dog colonies than random sites that year.

Across years and plot sizes, the perennial grass *Bouteloua curtipendula* was more frequent ($Q \geq 2.44$) on random sites than prairie dog colonies, while the perennial grass *Bouteloua gracilis* was more frequent ($P \leq 0.03$) on shortgrass sites than

Table 4. Mean frequencies ($\pm$ SE) of species that differed significantly among treatments during sampling of prairie dog colonies, non-colonized random sites and non-colonized shortgrass sites ($n = 13, 8$ and 6 , respectively) in Kansas and Colorado during 1997, as well as notable species which could not be statistically analyzed. Different superscripts within rows indicate significant differences ($P < 0.05$ or $Q > 2.39$) from pair-wise comparisons.

	Prairie Dog Colonies	Random Sites	Shortgrass Sites
0.10-m ² plots			
<i>Euphorbia</i> spp. ²	0.72 $\pm$ 0.07 ^a	0.23 $\pm$ 0.09 ^b	0.56 $\pm$ 0.09 ^a
<i>Sphaeralcea coccinea</i> (Pursh) Rydb.	0.35 $\pm$ 0.05 ^a	0.24 $\pm$ 0.04 ^a	0.14 $\pm$ 0.03 ^b
<i>Astragalus</i> spp. ¹	0.01 $\pm$ 0.01 ^a	0.02 $\pm$ 0.01 ^b	0.01 $\pm$ 0.01 ^{ab}
<i>Psoralea tenuifolia</i> Pursh	0.01 $\pm$ 0.01 ^a	0.09 $\pm$ 0.05 ^b	0.01 $\pm$ 0.01 ^{ab}
<i>Aristida purpurea</i> Nutt.	0.62 $\pm$ 0.07 ^a	0.24 $\pm$ 0.06 ^b	0.25 $\pm$ 0.04 ^b
<i>Bouteloua curtipendula</i> (Michx.) Torr.	0.01 $\pm$ 0.01 ^a	0.43 $\pm$ 0.12 ^b	0.10 $\pm$ 0.06 ^{ab}
<i>Bouteloua gracilis</i> (H. B. K.) Lag. ex Griffiths	0.38 $\pm$ 0.09 ^a	0.42 $\pm$ 0.08 ^a	0.81 $\pm$ 0.07 ^b
<i>Hordeum pusillum</i> Nutt.	0.05 $\pm$ 0.02 ^a	0.03 $\pm$ 0.01 ^a	0.16 $\pm$ 0.04 ^b
<i>Schedonnardus paniculatus</i> (Nutt.) Trel.	0.22 $\pm$ 0.04 ^a	0.08 $\pm$ 0.04 ^b	0.06 $\pm$ 0.03 ^b
<i>Sporobolus cryptandrus</i> (Torr.) A. Gray	0.03 $\pm$ 0.01 ^a	0.16 $\pm$ 0.05 ^b	0.08 $\pm$ 0.02 ^{ab}
10.0-m ² plots			
<i>Kochia scoparia</i> (L.) Schrad.	0.23 $\pm$ 0.05 ^a	0.03 $\pm$ 0.01 ^b	0.09 $\pm$ 0.04 ^{ab}
<i>Salsola</i> spp. ²	0.11 $\pm$ 0.03 ^a	0.01 $\pm$ 0.01 ^b	0.02 $\pm$ 0.01 ^b
<i>Dalea enneandra</i> Nutt.	0	0.06 $\pm$ 0.03 ^a	0.04 $\pm$ 0.03 ^a
<i>Psoralea tenuifolia</i> Pursh	0.12 $\pm$ 0.04 ^a	0.44 $\pm$ 0.11 ^b	0.18 $\pm$ 0.08 ^a
<i>Gaura coccinea</i> Pursh	0.11 $\pm$ 0.03 ^a	0.26 $\pm$ 0.05 ^b	0.07 $\pm$ 0.02 ^a
<i>Oenothera triloba</i> Nutt.	0.03 $\pm$ 0.02 ^a	0.02 $\pm$ 0.01 ^{ab}	0.06 $\pm$ 0.01 ^b
<i>Euphorbia stictospora</i> Engelm.	0.09 $\pm$ 0.03 ^a	0.01 $\pm$ 0.01 ^b	0.03 $\pm$ 0.02 ^{ab}
<i>Asclepias latifolia</i> (Torr.) Raf.	0.01 $\pm$ 0.01 ^a	0.03 $\pm$ 0.01 ^b	0.01 $\pm$ 0.01 ^{ab}
<i>Convulvulus equitans</i> Benth.	0.01 $\pm$ 0.01 ^a	0.04 $\pm$ 0.01 ^b	0.01 $\pm$ 0.01 ^a
<i>Cryptantha minima</i> Rydb.	0.14 $\pm$ 0.04	0	0
<i>Thelesperma</i> spp. ³	0.07 $\pm$ 0.07 ^a	0.19 $\pm$ 0.09 ^b	0.04 $\pm$ 0.02 ^{ab}
<i>Trapopogon dubius</i> Scop.	0.01 $\pm$ 0.01 ^a	0.07 $\pm$ 0.03 ^b	0.10 $\pm$ 0.04 ^b
<i>Aristida purpurea</i> Nutt.	0.87 $\pm$ 0.04 ^a	0.56 $\pm$ 0.09 ^b	0.72 $\pm$ 0.07 ^{ab}
<i>Bouteloua curtipendula</i> (Michx.) Torr.	0.04 $\pm$ 0.03 ^a	0.58 $\pm$ 0.13 ^b	0.18 $\pm$ 0.10 ^{ab}
<i>Bromus japonicus</i> Thunb. ex Murr.	0	0.16 $\pm$ 0.06 ^a	0.18 $\pm$ 0.14 ^a
<i>Buchloe dactyloides</i> (Nutt.) Engelm.	0.65 $\pm$ 0.08 ^a	0.32 $\pm$ 0.12 ^b	0.74 $\pm$ 0.07 ^a
<i>Hordeum pusillum</i> Nutt.	0.14 $\pm$ 0.04 ^{ab}	0.07 $\pm$ 0.03 ^a	0.45 $\pm$ 0.11 ^b
<i>Schedonnardus paniculatus</i> (Nutt.) Trel.	0.66 $\pm$ 0.06 ^a	0.22 $\pm$ 0.06 ^b	0.26 $\pm$ 0.06 ^b
<i>Sporobolus cryptandrus</i> (Torr.) A. Gray	0.10 $\pm$ 0.04 ^a	0.38 $\pm$ 0.09 ^b	0.37 $\pm$ 0.11 ^b

¹*Astragalus lotiflorus* Hook. and *A. nuttallianus* DC.

²*Salsola collina* Pall. and *S. iberica* Senn. & Pau

³*Thelesperma filifolium* (Hook.) A. Gray and *T. megapotamicum* (Spreng.) O. Ktze.

prairie dog colonies when the 0.10-m² plot was used both years. Use of both plot sizes indicated the perennial grass *Sporobolus cryptandrus* (Torr.) A. Gray was more frequent ($P < 0.01$) on random sites than prairie dog colonies in 1997.

Discussion

Numerous species were detected only on prairie dog colonies, or on only 1 of the non-colonized treatments, and statistical analyses was not possible for these and many others. Because the majority of these species were encountered so rarely, their presence or absence from any of the treatments is likely of no biological significance. However, some of these species deserve mention because when they did occur on 1 of the treatments, they were present in relatively high frequencies. This includes the annual forb *Cryptantha mini-*

ma, found solely on prairie dog colonies. Notable species found solely on non-colonized sites include the perennial forb *Dalea enneandra* Nutt., and the annual grass *Bromus japonicus*.

For many of the species examined in this study, differences in frequency among treatments were detected 1 year and not the other. This is likely explained by the great difference in precipitation amounts preceding each field season. Also, statistical analyses detected significant differences for some species using results from one plot size, but not the other. This is to be expected because density and dispersion characteristics of each species greatly influences the effectiveness of different sized plots used for statistical sampling (Hyder et al. 1963, 1965), and we used 2 plot sizes to account for these differences.

While analyses of the diversity indices indicated no significant differences among the treatments, analyses of the cover and frequency data revealed numerous differ-

ences, and definite trends in the data are evident. Prairie dog colonies tended to be characterized by higher cover and frequencies of perennial shortgrasses and annual forbs, whereas non-colonized random sites were characterized by higher cover and frequencies of perennial mid-height grasses and perennial forbs. Other studies have reported comparable results. Research in South Dakota (Coppock et al. 1983, Agnew et al. 1986, Archer et al. 1987) and Texas (Weltzin et al. 1997b) has consistently reported higher cover values, frequencies and biomass of mid-height grasses on non-colonized mixed-grass prairie relative to prairie dog colonies. In Colorado, Bonham and Lerwick (1976) reported higher cover of annual forbs on prairie dog colonies than in non-colonized shortgrass prairie. Likewise, in South Dakota, Archer et al. (1987) reported higher frequencies of annual forbs on prairie dog colonies than in non-colonized mixed-grass prairie. Finally, Weltzin et al. (1997b) reported that prairie dog colonies were characterized by significantly lower biomass of perennial forbs and annual grasses than non-colonized mixed-grass prairie in Texas.

Composition differences in the vegetation of prairie dog colonies and non-colonized sites are likely explained by differences in the frequency and intensity of herbivory and soil disturbance. Although graminoids tend to comprise the bulk of prairie dog diets (Hansen and Gold 1977, Summers and Linder 1978, Fagerstone et al. 1981, Wydeven and Dahlgren 1982, Uresk 1984), herbivory pressure on all vegetation within colonies should be intense, relative to non-colonized grassland. Prairie dogs can defoliate plants at the ground surface and they will dig into the soil to expose plant tissue after above-ground parts have been removed (King 1955, Koford 1958, Smith 1967). Additionally, prairie dogs forage within the confines of the colony throughout the year, so plants may be defoliated season-long, year after year. We do not know the exact ages of the colonies we sampled. However, others have demonstrated that longer periods of occupancy by prairie dogs results in greater compositional and structural contrasts between prairie dog colonies and non-colonized areas (Coppock et al. 1983, Archer et al. 1987).

The perennial grasses that dominated prairie dog colonies in this study were characterized by traits that should be beneficial in environments characterized by high rates of herbivory. These include a short stature (*Bouteloua gracilis* and

Buchloe dactyloides), a sprawling habit (*Schedonnardus paniculatus*), and sharp-tipped awns (*Aristida purpurea*). *Buchloe dactyloides* has also been shown to be very tolerant of high rates of cattle herbivory (Klipple and Costello 1960, Launchbaugh 1967, Hart and Ashby 1998). The non-colonized random sites were characterized by taller grasses such as *Bouteloua curtipendula* and *Sporobolus cryptandrus*. The extreme herbivory pressures on prairie dog colonies likely reduces the competitive influence of many species within a colony (e.g. *Bouteloua curtipendula*), allowing species which are less palatable, or exceptionally adept at avoiding or tolerating herbivory, to experience competitive release (e.g. *Buchloe dactyloides* and *Aristida purpurea*). Differences that we detected in graminoid composition, vegetation height and visual obstruction suggest there may be less forage available for cattle on prairie dog colonies relative to non-colonized areas. However, others have argued that because a large proportion of the forage within a colony is high quality regrowth, reductions in forage quantity on colonies is compensated by an increase in forage quality (O'Meilia et al. 1982, Coppock et al. 1983, Krueger 1986).

The burrowing, digging and scratching of soil by prairie dogs may also benefit species which compete poorly with dominating perennial vegetation. Small-scale soil disturbances in shortgrass prairie have been described as "safe sites" where the overwhelming competitive effects of perennial grasses are greatly reduced (Milchunas et al. 1992, Aguilera and Lauenroth 1995). Bare and disturbed soils within prairie dog colonies may provide "safe sites" for ruderal species that can avoid or tolerate prairie dog herbivory (e.g. *Amaranthus* spp., *Euphorbia* spp., *Salsola* spp., *Kochia scoparia* and *Cryptantha minima*). While our methods were not suitable for identifying whether ruderal species were actually growing in areas of disturbed soil within a prairie dog colony, as opposed to growing within undisturbed sod, our results demonstrate that prairie dog colonies provided superior environments, relative to non-colonized areas, for many of these species.

Shortgrass prairie vegetation is considered well adapted to the herbivory of large ungulates (Mack and Thompson 1982, Milchunas et al. 1988, 1998, Hart and Ashby 1998). In shortgrass prairie, cattle grazing can homogenize vegetation, in part because the already dominant short-grasses increase their dominance in

response to herbivory (Milchunas et al. 1988, 1992, 1998, Milchunas and Lauenroth 1989). The effects of intense grazing and soil disturbance by prairie dogs on shortgrass prairie may counter the homogenizing effects of cattle grazing. The importance of prairie dogs in promoting heterogeneity in shortgrass landscapes has been asserted by others (Knopf and Sampson 1997), in part because colonies occur at a much larger scale than other disturbances in shortgrass prairie, such as cattle fecal pats, harvester ant nest sites, gopher mounds, small mammal diggings, and areas infested with root feeding beetle larvae (Coffin and Lauenroth 1988, Martinsen et al. 1990, Milchunas et al. 1992).

We found numerous differences among the vegetation of prairie dog colonies and non-colonized areas, especially when prairie dog colonies were compared to random sites. We conclude that prairie dogs influence shortgrass prairie in a manner which causes the vegetation of colonies to be distinct from that of adjacent non-colonized areas. However, in spite of these differences, our results also lead us to conclude that prairie dogs do not substantially alter the essential character of shortgrass vegetation. While frequencies of various plant components were altered on prairie dog colonies, and some lesser components were missing, all of the components typical of the region's vegetation were present. Colonies were dominated by perennial warm-season grasses characteristic of a shortgrass region, and colonies had similar amounts of bare ground when compared to non-colonized sites.

Shortgrass prairie is considered well adapted to the herbivory of large ungulates. We suggest shortgrass prairie is also well adapted to the levels of prairie dog herbivory and soil disturbance that were present at our study sites. While prairie dogs undoubtedly alter shortgrass prairie, they are one of many forces and disturbances that have shaped and defined the vegetation of this region, and prairie dog colonies represent one point along a gradient which depicts the range of variability for shortgrass vegetation.

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Vegetation dynamics following seasonal fires in mixed mesquite/acacia savannas

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Abstract

Fires were once a natural part of most savanna ecosystems, but lack of fine fuel and an active suppression policy have changed fire frequency and seasonality. Re-introducing fires to these systems has been touted as a cost-effective means to reduce woody cover while increasing herbaceous growth. We compared the effects of single, recurring annual, and biennial fires on the vegetation dynamics of a mixed mesquite/acacia (*Prosopis/Acacia*) savanna in southern Texas. Fires were conducted either during the growing season or the dormant season from 1991 through 1995. Some of the fire treatments were statistically unreplicated to permit a sufficient plot size for natural fire behavior. All plots showed a successional trajectory from short-grasses towards mid-grasses regardless of the fire season or frequency. The population size structure of perennial grasses was unaffected by the fires, with the basal area of most plants being less than 25 cm². Forb diversity was high with over 100 different species identified in the experimental area. Forb composition, however, was unaffected by either the season or frequency of fire, but was related to the year of observation. Shrubs in this community typically sprout after disturbance, so little mortality was expected. The only observed mortality was of small shrubs or saplings (diameter < 3 cm) and of large trees which had woodrat (*Neotoma micropus*) nests at the base. Reintroducing growing season fires into mesquite/mixed acacia shrublands did not conclusively alter plant community composition. Burning during the growing season when environmental conditions were hotter and drier did not accelerate succession toward grass-dominated communities.

Key Words: fire frequency, seasonality, prescribed burns, *Prosopis glandulosa*, *Acacia*, detrended correspondence analysis, ordination

The mixed mesquite/acacia (*Prosopis/Acacia*) savannas of southwestern North America have undergone a drastic change in physiognomy over the last 200 years. These previously open savannas are now dominated by low shrubs with a honey mesquite (*Prosopis glandulosa* var. *glandulosa* Torr) overstory. Fires were once a natural occurrence in these savannas, but fire frequency has decreased due to reductions in fine fuel and to fire

Resumen

Los incendios constituyeron un fenómeno natural en la mayoría de los ecosistemas de sabanas, pero debido a la restricción de medidas de mantenimiento y a la falta de combustibles finos, han cambiado su frecuencia y estacionalidad. La reintroducción de incendios en estos sistemas ha sido considerada como una medida económicamente efectiva para reducir la vegetación leñosa y así aumentar la capa herbácea. Este estudio compara el efecto de diferentes frecuencias de incendios (anual, múltiples por año, a bianual) sobre la dinámica de la vegetación en una sabana constituida por una combinación de mesquite/acacia (*Prosopis/Acacia*) del sur de Texas. Los incendios fueron realizados durante las estaciones de crecimiento o reposo durante 1991 a 1995. Para permitir un tamaño suficiente de las parcelas, algunos tratamientos no fueron repetidos estadísticamente. Todas las parcelas mostraron una trayectoria en sucesión de pastos bajo a pastos medianos, respuesta que fue independiente de la frecuencia o estacionalidad de los incendios. La estructura y tamaño de la población de los pastos perennes no fueron afectados por los incendios, presentando la mayoría de las plantas un área basal menor a 25 cm². La diversidad de pastos fue alta, con más de 100 especies identificadas en el área experimental. La composición de los pastos no fue afectada por la estación o frecuencia de incendios, pero estuvo en relación con el año de observación. La comunidad arbustiva brotó después del fuego, no existiendo prácticamente mortalidad; sólo se observó mortalidad en los arbustos de menor porte (con diámetros $\leq$ 3 cm) y en árboles de gran porte que tenían nidos de ratas (*Neotoma micropus*) en la base. La reintroducción de incendios durante el período de crecimiento vegetativo para la combinación arbustiva de mesquite/especies de acacia no alteró la composición de la comunidad de plantas. La realización de incendios durante el período de crecimiento, en condiciones ambientales de altas temperaturas y baja humedad, no aceleró el desarrollo de las comunidades herbáceas.

suppression policy. Where fires are used for brush management, prescribed burns are conducted during the cooler dormant season months when fire control is easier (Scifres and Hamilton 1993).

There is growing evidence in other ecosystems, however that frequency and seasonality of fires can affect fire intensity (Williams et al. 1999) and alter herbaceous species composition (Howe 1994, 1995, Tveten and Fonda 1999). Dormant season fires conducted in mesic communities of the northern Great Plains favor C4 grasses (Howe 2000) and forbs (Biondini et al. 1989) whereas growing-season fires promote C3 grasses (Howe 1995, 2000). In xeric communities of desert grasslands, fires can

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shift the balance between black grama (*Bouteloua eriopoda* Torr.) and blue grama (*Bouteloua gracilis* (Kunth.) Lag. ex Griffiths) within the herbaceous layer (Gosz and Gosz 1996).

There is little likelihood, however, that fires conducted during the dormant season will reduce the density and long-term cover of resprouting shrubs (Engle et al. 1991, Boo et al. 1997, Grice 1997, Pendergrass et al. 1998). A more realistic effect of fires may be a change in plant architecture. Low intensity dormant-season fires in mesquite communities of north Texas killed low branches on large shrubs or small trees while not affecting apical dominance, whereas high intensity summer fires killed more of the canopy resulting in basal sprouting and development of mesquite thickets (Ansley and Jacoby 1998).

The objectives of this study were to determine the impact of fire seasonality and fire frequency on plant community changes within mesquite/acacia shrublands. Successional trajectories of density and cover were modeled for shrubs, grasses and forbs through a series of annual and biennial seasonal fires. Changes in the basal area size classes of perennial grasses were determined after these fires to monitor population structure dynamics.

Methods

The study was conducted in a mesquite/mixed brush community on the Lyles Experimental Ranch near Uvalde, Tex (29° 03' N, 95° 54' W). This area is semiarid with a mean annual precipitation (96 year record) of 61.7 cm distributed bimodally with peaks in May–June and September. Annual extremes over the 96 year period range from 23.6 to 114.4 cm. Precipitation during the study was greater than average for 3 years (1990, 1992, and 1994) and below average for 2 years (1991 and 1993, Fig. 1).

An 80-ha area was subdivided into 2 equal parts for growing season (July–August) or dormant season (January–February) prescribed fires. Each of these seasonal areas was further subdivided and randomly assigned to 1 of 3 treatments resulting in 13-ha study plots. The first area was an unburned control, the second was burned on an annual cycle and the third was burned on a biennial cycle. The decision was made to create plots large enough for normal fire behavior although this design resulted in a non-replicated experiment. Statistical analyses, described in more detail in a

Fig. 1. Monthly precipitation (bars) from the Lyles Experimental Ranch for the duration of the study (1990–1994) and the long-term average (1904–1994, solid line) of the Uvalde, Tex. weather station approximately 30 km from the study site.

later section, used the techniques presented in Milliken and Johnson (1989) for planned, unreplicated experiments.

Prior to any burning, shrub and tree canopy cover was measured along 12 permanent 15-m lines in each area (total $n = 72$) using the line intercept method (Canfield 1941). Grass density was measured in 30 permanent 1-m² plots within each treatment. The number of plants within each plot in 3 basal area cover classes (<25, 25–50, and >50 cm²) were counted for each grass species. Density was used rather than canopy cover for the grasses to detect changes in plant size and fragmentation. Forb cover was estimated using Daubenmire frames (20 x 50 cm) located in each corner of the permanent grass plots for a total of 120 forb plots in each of the treatment areas. All plots and transects were resampled annually in either June or July from 1990 through 1994. The sample in June 1990 served as the pre-burn sample for all plots. Nomenclature follows Hatch et al. (1990).

Livestock grazing on this site was discontinued in 1988 to allow an accumulation of fine fuel, and livestock were excluded for the duration of this study as well. Prior to the experiment, this pasture was used as a trap to hold a large number of animals for a short period of time. Potential stocking rate prior to this experiment was very low (> 45 acres per animal unit) due to heavy brush cover.

Environmental conditions during dormant-season (January–February) burns were air temperatures of 7–18°C, wind speed of 1.3–4.5 m sec⁻¹ from the southeast, and relative humidity of 65–80%. Growing season fires (July–August) were conducted with air temperatures of 35–40°C, wind speed of 2.2–5.4 m sec⁻¹ from the southeast, and relative humidity of 20–50%. Fine fuel on all sites ranged from 450 to 890 kg ha⁻¹ and was spatially discontinuous. Firelines were widened with backfires, and the main burns were conducted as headfires. All plots in the biennial cycle were burned twice, plots in the dormant season-annual cycle were burned 4 times, and plots in the growing season-annual cycle were burned 3 times (Table 1). All permanent plots were inspected immediately after each fire to make sure they had burned, and if the area had not burned then new fires were started.

The trajectory of plant community changes within each of the 6 burn treatments was analyzed using detrended correspondence analysis (DECORANA) with the PC-ORD software package (MJM Software). This version of the PC-ORD program contained corrected algorithms to minimize distortion of the axes. Separate analyses were conducted for shrubs, grasses, and forbs because of the different sampling techniques used for each life form. Species with only 1 occurrence were deleted from the matrix prior to ordina-

Table 1. Sampling and burning schedule within a mesquite/acacia shrubland in the Rio Grande Plains of Texas for different fire seasons and intervals.

Fire Season	Fire Interval	1990	1991		1992		1993		1994	
		Jun	Feb	Jun	Jan	Jul	Jan	Jul	Jan	Jul
Growing	Biennial	S		S _{2,4,6} B		S _{2,4,6}		S _{4,6} B		S ₆
	Annual	S		S _{2,4,6} B		S _{2,4,6} B		S _{4,6} B		S ₆
	Control	S ₁		S _{1,2,4,6}		S _{2,4,6}		S _{4,6}		S ₆
Dormant	Control	S _{1,3,5}		S _{1,2,3,5}		S _{2,3,5}		S ₅		S ₅
	Annual	S _{1,3,5}	B	S _{1,3,5}	B	S _{3,5}	B	S ₅	B	S ₅
	Biennial	S _{1,3,5}	B	S _{1,3,5}		S _{3,5}	B	S ₅		S ₅

S = Sampled, B = Burned, Subscripts refer to the ANOVA models described in the text.

tion, and rare species (< 10 observations) were downweighted to minimize their impact on the ordination (Hill and Gauch 1980). The ordination of each treatment/year combination (n = 24) allowed the establishment of trajectories of species change through time (Abrahamson and Abrahamson 1996, Fuhlendorf and Smeins 1997).

Changes in the population structure of grasses in different basal area size classes were analyzed with a series of 6 separate analyses. These analyses were conducted to detect changes in the size class distribution of the grass community that may not be reflected in changes of total cover (e.g. total cover could be the same with many small plants or a few large plants). The first ANOVA tested for the effects of a single dormant-season fire by using plots from the unburned areas as replicated controls and the samples from June 1990 and June 1991 on the annual and biennial cycle dormant-season areas as replicated

treatments (Table 1). The biennial cycle areas had been burned only once at this point so they could be used as a replicate plot of the annual burn. The statistical model used 2 replications, burn treatment (single or none), basal area cover classes and their interaction (error A) in the main model and the 2 observation times as a split plot (4-way interaction = error B). A split-plot model was used, rather than a repeated measures model, after statistical consultation and sphericity tests. The second ANOVA tested the effect of a single growing-season fire using the unburned control areas and the samples from June 1991 and July 1992 observations from the annual and biennial cycle areas within the growing-season fire area as the treatment (Table 1). The same statistical model was used as for the single dormant-season fires. All tests were conducted with a significance level of P < 0.05.

Logistical constraints in the amount of area available to burn and in field sam-

pling time prevented true replication of the biennial burning treatments. Analysis of unreplicated experiments is possible if interaction terms are assumed to be zero and if higher order interactions are used as error terms (Milliken and Johnson 1989). Interpretation of the results should be done with care, and extrapolations should be performed with some trepidation (Mead 1988). The third ANOVA tested the effects of unburned, a single, and 2 consecutive dormant-season burns using samples from the control, annual and biennial cycle areas from June 1990 through July 1992 (Table 1). The statistical model used burn treatment (none, single or biennial), basal area cover classes and their interaction (error A) in the main model and the 2 observation times as a split plot (3-way interaction = error B). A similar analysis (ANOVA 4) for growing season fires used samples from the control, annual, and biennial cycle areas from June 1991 through July 1993 (Table 1). Finally, the

Table 2. Mean percent cover of woody vegetation in a mesquite/mixed acacia shrubland in the Rio Grande Plains of Texas prior to implementing fire treatments in June 1990.

Species	Abbr.	Dormant-Season			Growing-Season		
		Fire Frequency			Fire Frequency		
		Unburned	Annual	Biennial	Unburned	Annual	Biennial
<i>Acacia berlandieri</i>	ACBE	1.4	3.2	1.6	3.0	1.4	4.1
<i>Acacia greggii</i>	ACGR	0.2	1.5	2.6	0.7	2.3	2.0
<i>Acacia schaffneri</i>	ACSC	3.7	4.4	7.8	13.1	2.1	9.0
<i>Acacia wrightii</i>	ACWR	—	—	0.1	—	—	—
<i>Aloysia gratissima</i>	ALGR	4.3	1.5	1.6	2.1	0.6	2.3
<i>Castela texanum</i>	CATE	—	—	—	—	0.4	—
<i>Celtis pallida</i>	CEPA	0.1	—	1.2	0.8	0.1	2.7
<i>Condalia ericoides</i>	COER	—	1.7	—	—	—	—
<i>Condalia hookeri</i>	COHO	1.9	—	1.6	0.1	2.2	0.9
<i>Colubrina texensis</i>	COTE	0.7	2.7	1.6	0.1	—	—
<i>Diospyros texana</i>	DITE	1.8	—	—	0.3	1.1	0.1
<i>Ephedra antisyphilitica</i>	EPAN	0.2	—	0.3	0.5	—	0.1
<i>Guaiacum angustifolium</i>	GUAN	1.6	1.4	2.7	1.8	0.3	1.2
<i>Leucophyllum frutescens</i>	LEFR	—	—	—	—	1.3	—
<i>Lycium berlandieri</i>	LYBE	1.8	1.5	3.4	4.2	4.6	2.9
<i>Lycium carolinianum</i>	LYCA	—	—	0.2	—	—	0.5
<i>Parkinsonia texana</i>	PATE	0.2	—	0.3	—	0.3	—
<i>Prosopis glandulosa</i>	PRGL	44.7	37.2	31.3	17.2	19.0	18.2
<i>Rhus microphylla</i>	RHMI	0.8	0.5	2.4	1.8	3.1	1.6
<i>Schaefferia cuneifolia</i>	SCCU	0.7	0.2	1.1	2.1	0.7	0.8
<i>Yucca treculeana</i>	YUTR	—	—	0.2	—	—	—
<i>Zizyphus obtusifolia</i>	ZIOB	0.7	0.2	0.6	0.1	0.3	0.9
Total		64.8	56.1	60.6	47.9	39.8	47.4

Fig. 2. Detrended correspondence analysis of shrub cover (A) and species distribution in the ordination space (B) within a mesquite/mixed acacia shrubland in the Rio Grande Plains of Texas after growing-season (GS) and dormant-season (DS) fires. Numbers within the figure designate the year of observation beginning in 1990 and the lines represent the trajectory of change. Species acronyms are defined in Table 2.

effects of recurring annual versus recurring biennial fires were tested using the samples from June 1990 through July 1994 for the dormant season fires (ANOVA 5) and from June 1991 through July 1994 for the growing season fires (ANOVA6). No mean separation tests were planned with these analyses due to the lack of true replication.

Results

Woody Vegetation

Prior to the treatment application, 24 species of woody shrubs and trees with total cover ranging from 39.8 to 64.8% were identified within the 6 treatment areas (Table 2, shrubs with trace amounts (< 0.01%) not shown). Honey mesquite

was the dominant tree on all sites with cover ranging from a high of nearly 44% on the dormant-season control area to a low of 17% on the growing-season control area. The most common shrub was twisted acacia (*Acacia schaffneri* (S. Wats) Herm. var *bravoensis*), while most other shrubs had less than 10% cover. Seven species appeared in only a single treatment area. Shrub and tree cover were not affected by treatments ($P > 0.1$), so only the initial cover values are presented.

Although the treatment areas all started with slightly different species compositions, trajectories showed little change in the woody vegetation due to any of the burning frequencies or seasons (Fig 2A). The Axis 1 (eigenvalue = 0.105, length = .824) represented a gradient away from mesquite and Texas colubrina (*Colubrina*

Fig. 3. Detrended correspondence analysis of grass density (A) and species distribution in the ordination space (B) within a mesquite/mixed acacia shrubland in the Rio Grande Plains of Texas after growing-season (GS) and dormant-season (DS) fires. Numbers within the figure designate the year of observation beginning in 1990 and the lines represent the trajectory of change. Species acronyms are defined in Table 3.

texana T.&G.) and towards an increasing mixture of resprouting, medium-stature shrubs common on deep soils [guajillo (*Acacia berlandieri* Benth.), twisted acacia, and spiny hackberry (*Celtis pallida* Torr.)] (Fig 2B). Axis 2 (eigenvalue = 0.051, length=.742) represented a gradient from the same medium-statured shrubs as in Axis 1 towards shrubs common on shallow soils which do not resprout [cieniza (*Leucophyllum frutescens* (Berl.) I.M. Johnst.)] or which resprout slowly [allthorn (*Castela texanum* (T.&G.) Rose), and Texas paloverde (*Parkinsonia texana* (Gray) S.Wats.)]. Small shrubs (< 0.5 m tall and < 2.5 cm diameter) were killed by both growing-season and dormant-season fires but the only mortality among mature trees occurred when woodrats (*Neotoma micropus*) nested at the base. The addition-

Table 3. Grass density (# m⁻²) in a mesquite/mixed acacia shrubland in the Rio Grande Plains of Texas prior to prescribed fires (Year 0 in June 1990) and at the end of the study (Year 4 in July 1994).

		Dormant-Season						Growing-Season					
Fire Frequency		Unburned		Annual		Biennial		Unburned		Annual		Biennial	
Year	Abbr.	0	4	0	4	0	4	0	4	0	4	0	4
Sub Canopy grasses		----- (no m ⁻²) -----											
<i>Digitaria cognata</i>	DICO	1.5	5.0	4.1	4.0	3.3	1.5	2.7	2.0	1.0	–	5.5	6.0
<i>Eragrostis intermedia</i>	ERIN	5.6	3.0	1.1	5.6	3.5	5.0	2.2	1.7	3.0	1.3	4.1	2.4
<i>Pappophorum vaginatum</i>	PAVA	1.7	0	1.0	–	20.2	–	5.0	–	1.3	–	–	–
<i>Setaria leucopila</i>	SELE	4.2	5.0	3.9	7.0	2.3	1.3	3.8	4.0	2.5	3.5	2.8	1.0
<i>Setaria texana</i>	SETE	3.0	2.2	2.2	3.8	4.3	3.5	6.0	3.3	–	1.2	2.0	2.8
<i>Tridens eragrostoides</i>	TRIN	4.4	6.1	5.3	6.4	7.3	4.2	2.7	3.3	5.0	1.9	3.3	5.9
<i>Tridens texanus</i>	TRTE	4.0	0	10.9	6.0	5.5	–	2.7	–	3.0	–	1.8	–
<i>Chloris verticillata</i>	CHVE	–	–	–	–	1.0	1.0	–	–	4.0	–	–	–
<i>Pappophorum bicolor</i>	PABI	–	5.7	–	6.0	1.0	11.0	–	6.0	1.0	12.0	–	–
<i>Stipa leucotricha</i>	STLE	2.0	3.3	7.3	3.8	1.0	–	–	1.0	6.0	5.2	–	2.0
<i>Eragrostis curtispedicellata</i>	ERCU	–	4.0	–	2.0	–	1.7	–	–	–	3.3	–	–
<i>Chloris subdoliclostachya</i>	CHSU	–	–	–	–	–	–	–	–	1.0	–	–	–
<i>Schizachyrium scoparium</i>	SCSC	–	9.5	–	–	–	–	–	–	–	–	–	–
<i>Bothriochloa pertusa</i>	BOPE	–	2	1.0	–	–	1.5	–	–	–	–	–	–
<i>Hordeum pusillum</i>	HOPU	–	–	–	–	–	–	–	–	107	–	–	–
Interstitial grasses													
<i>Aristida purpurea</i>	ARPU	8.6	5.2	14.7	4.4	15.6	11.0	12.2	8.8	31.2	10.5	13.5	6.6
<i>Bothriochloa saccharoides</i>	BOSA	–	–	1.0	–	1.3	–	2.0	7.0	1.0	–	1.0	–
<i>Bouteloua trifida</i>	BOTR	68.2	8.1	33.2	4.2	44.0	6.6	27.4	14.3	31.4	8.2	39.4	8.9
<i>Buchloe dactyloides</i>	BUDA	1.0	0	23.0	–	–	–	11.0	–	–	–	36.5	–
<i>Hilaria belangeri</i>	HIBE	22.0	17.3	6.0	9.0	34.0	–	15.8	14.8	4.5	6.8	22.1	15.5
<i>Sporobolus cryptandrus</i>	SPCU	–	–	–	–	–	–	1.0	1.0	–	–	–	2.0
<i>Tridens muticus</i>	TRMU	7.9	6.9	24.3	7.8	6.2	7.4	5.8	4.0	15.7	3.2	5.9	3.6
<i>Tridens albescens</i>	TRAL	–	–	–	–	–	–	–	–	5.0	–	–	–
<i>Bouteloua rigidiseta</i>	BORI	–	1.8	–	–	–	–	–	–	–	–	3.0	1.5
<i>Bothriochloa ischaemum</i>	BOIS	–	–	–	–	–	1.5	–	–	–	–	–	–
Both locations													
<i>Panicum hallii</i>	PAHA	3.1	1.4	4.7	1.4	4.6	1.0	3.6	1.7	4.2	1.0	3.1	2.0
<i>Panicum obtusum</i>	PAOB	–	2.0	7.3	6.0	14.5	5.4	–	1.0	–	–	–	–
<i>Bromus unioloides</i>	BRUN	–	–	–	–	–	–	–	–	–	4.0	1.0	–

al fuel allowed the fires to burn throughout the root crown and kill the tree. The loss of small trees and shrubs was not sufficient to cause a detectable change in woody plant canopy cover.

Grasses

Prior to treatment application, 33 species of grasses were identified in the permanent plots, with 5 occurring in trace amounts (Table 3). Only 2 species, little barley (*Hordeum pusillum* Nutt.) and rescuegrass (*Bromus unioloides* Kunth), were annuals, while the remainder were perennials. The grasses with the greatest density were Wrights threeawn (*Aristida purpurea* Nutt.), red grama (*Bouteloua trifida* Thurb.), and common curlymesquite (*Hilaria belangeri* (Steud.) Nash). All 3 grasses were common in interstitial areas between mesquite trees and shrub clusters. Wrights threeawn and red grama are bunchgrasses and common curlymesquite is stoloniferous. Mid-grasses common under tree and shrub canopies included Texas bristlegrass (*Setaria texana* W.H.P. Emery), southwestern bristlegrass (*S.*

scheelei (Steud.) A.S. Hitchc.), plains lovegrass (*Eragrostis intermedia* A.S. Hitchc.), and lovegrass tridens (*Tridens eragrostoides* (Vasey and Scribn.) Nash.).

Two eigenvectors were significant in the ordination ($P < 0.1$, Fig 3A). Axis 1 (eigenvalue = 0.190, length = 1.39) represented a gradient away from species found in the interstitial spaces between mesquite trees [Wright's threeawn, red grama, curlymesquite and white tridens (*Tridens albescens*)] towards species found on moist sites [lovegrass tridens, vine mesquite (*Panicum obtusum* Kunth), and bristlegrass (*Setaria leucopila* Scribn. & Merr.) (Fig. 3B). Axis 2 (eigenvalue = 0.111, length 1.235) represented a movement from short-grasses towards mid-grass species found under mesquite trees [pink pappusgrass (*Pappophorum bicolor* Fourn.) and gummy lovegrass (*Eragrostis curtispedicellata* Buckl.)]. All of the plots showed a trajectory away from short grasses and towards mid-grasses over the course of the experiment (Fig 3A and B). The plots showing the greatest change were dominated by shortgrasses at the beginning

of the experiment, but frequency of burning did not affect the trajectory of change.

Forbs

Eighty-eight forb species were found in more than a single permanent plot, and an additional 20 species occurred in only single plots (data not shown). Although 3 eigenvectors were significant, the first 2 accounted for most of the variation in forb cover (eigenvalues of 0.221 and 0.125 and lengths of 1.731 and 1.614, respectively, Fig. 4). Species common on disturbed sites were found at low values of Axis 2 and high values of Axis 1 while forb species used as wildlife forage [Indianmallow (*Abutilon fruticosum* Pen. & Rich.), Leatherweed croton (*Croton pottsii* L.), slender fleabane (*Erigeron tenuis* L.)] were found at high values of both Axis 1 and Axis 2. There were no discernible patterns to the trajectories of forb cover due to either season or frequency of burning (Fig. 4). Forb composition appeared to be more affected by year effects than by any treatment. Observations from each year tended to group together regardless of burning treatment.

Fig. 4. Detrended correspondence analysis of forb cover within a mesquite/mixed acacia shrubland in the Rio Grande Plains of Texas after growing-season (GS) and dormant-season (DS) fires. Numbers within the figure designate the year of observation beginning in 1990.

Grass population structure

Single fires, whether conducted during the dormant or growing season, did not affect the distribution among size classes of perennial grasses (Fig. 5, treatment by observation interaction term; $F_{1,8} = 1.84$ and $F_{1,8} = 0.16$, dormant and growing season, respectively). Fewer small plants ($<25\text{cm}^2$) occurred on burned plots after the fires, but they also decreased on the control plots. The number of medium-sized and large plants was low and remained constant on all treatments over the 2 years.

Burning in 2 successive years did not change the size class distribution of grasses compared to burning in a single year, or to not burning at all during either the growing-season (fire frequency by time interaction, $F_{4,8} = 0.67$), or the dormant-season (fire frequency by time interaction, $F_{4,8} = 0.73$). The density of small plants decreased in all treatments, but the number of medium-sized plants increased at the same time (data not shown). This suggests that plants were simply growing from one size class to another, regardless of the season or frequency of fire.

Recurring fires, where plots were burned every year for 4 years or burned every other year for 4 years, did not affect the size class distribution of grasses (fire frequency by time interaction, $F_{6,11} = 0.89$ and $F_{6,11} = 0.74$ for growing-season and

dormant-season fires, respectively). Plant densities were greatest in the small size class and approximately equal for the medium-sized and large plants among all treatments.

Discussion

Growing season fires typically generate more heat with greater flame length, rate of spread, and fireline intensity than dormant season fires (Sapsis and Kauffman 1991, Ansley et al. 1995, Williams et al. 1999). These growing season fires directly alter the plant's environment by increasing soil hardness, decreasing surface soil water content, and increasing soil temperatures through increased radiation loads (Daowei and Ripley 1997). In addition, fires which occur when the plant is physiologically active should be more likely to damage a plant than when the plant is dormant (Daubenmire 1968). It would seem therefore that growing season fires should have more of an effect than dormant season fires on community stability and succession. In fact, growing season fires can increase germination of some woody species (Hodgkinson 1991) and may promote herbaceous species diversity in some instances (Howe 1994, 1995). In this study, however, there was no change in the number of forb species following

either growing-season or dormant-season fires as compared to unburned controls. There are 2 possible explanations for this observation. First, the number of forb species was already high with over 100 species found in this 80-ha area, so an increase in diversity was unlikely; or second, the forb component of this ecosystem is driven more by annual weather patterns than by occasional disturbances such as fire. The grouping of the years of observations in the ordination space (Fig. 4) suggests that annual weather patterns were probably the driving variable for the forb component of this community.

Most of the grasses on this study site were C4 grasses, with the exception of Texas wintergrass (*Stipa leuchotricha* Trin & Rupr.) and little barley. Short-grasses were spatially limited to the interstitial areas while mid-grasses were common under the canopies of mature mesquite trees. Neither growing-season nor dormant-season fires caused a shift in the distribution of size classes among the grasses. Most of the grass population (93%) was in the $<25\text{cm}^2$ basal area class, and changes were only noted when plants grew into the next larger size class. All plots, burned and unburned, showed a trajectory from short-grasses to mid-grasses over the 5 year study. The control and biennial burning cycle of the dormant season treatments had the greatest shift in composition towards mid-grasses as evidenced by the greatest Euclidean distance between the beginning and end of the experiment in the ordinations (Fig 3A). These areas were generally in lower ecological condition than other areas at the beginning of the experiment. The changes in the grass component were more likely due to the absence of livestock grazing over a 5 year period than from any of the fire regimes. This area had been used as a trap for holding livestock and was heavily grazed prior to this study. The observation that burned and control treatments experienced similar dynamics, supports the hypothesis of a grazing release effect.

Single or recurring fires rarely decrease the density or abundance of resprouting shrubs and trees (Grice 1997, Ansley and Jacoby 1998, Sparks et al. 1998, Pendergrass et al. 1998). We observed little mortality of shrubs within the burned areas and there was little movement in the ordination space (Fig 2A). The shrub component remained at about the same composition from the beginning to the end of the experiment. The stability of the shrub component was similar to reports from a variety of different ecosystems including

Fig. 5. The distribution of perennial grasses among 3 basal area size classes following growing-season and dormant-season prescribed fires in a mesquite/mixed acacia shrubland in the Rio Grande Plains of Texas. Year 0 refers to the samples prior to the prescribed fires (1990) and Year 1 is the first growing season after the fires (1991). Control plots were not burned. Error bars denote ± 1 SE.

short-leaf pine (*Pinus echinata*) communities (Sparks et al. 1998), Willamette Valley prairies (Pendergrass et al. 1998), north Australian woodlands (Grice 1997), and Sierra Nevada mixed conifers (Kauffman and Martin 1990). In all of these plant communities, plant mortality was generally <10% for resprouting species although stem mortality was somewhat higher than that.

Fire frequency was expected to accelerate grass and forb composition change, but not expected to alter shrub composition (Ansley and Jacoby 1998). Our annual burn cycle was meant to mimic the most severe fire cycle, but we found no differences in grass density or forb cover between the annual and biennial fire cycles. Burning annually would require grazing restrictions to accumulate fine fuel, but plant responses would still mimic those of the biennial fire cycle.

Our findings may be related more to fire intensity than to frequency or seasonality.

High intensity fires cause more bare ground and greater recruitment (Hodgkinson 1991), and may have a more severe impact on plant population dynamics. Fuel loads on this site were low (450 to 890 kg ha⁻¹), but more importantly they were discontinuous so the rate of spread was low. The fires were therefore low intensity fires (although fireline intensity was not measured) which may kill small shrubs and low branches on large shrubs or trees (Ansley and Jacoby 1998), but should not alter shrub community composition. The relative importance of fire intensity rather than fire season has also been demonstrated in longleaf pine savannas in Florida (Glitzenstein et al. 1995) and in oak woodland in Oklahoma (Engle et al. 1996).

Reintroducing growing season fires into mesquite/mixed acacia shrublands did not conclusively alter plant community composition. Movement from a short-grass dominated site to mid-grasses was evident

in both burned and unburned plots suggesting that the cessation of grazing for 5 years was an important factor. When compared to the ungrazed controls, burning during the growing season with hotter and drier conditions did not accelerate change to a grass dominated community. We suggest that annual or biennial burns, either during the growing season or the dormant season, are not effective tools for stimulating the conversion of a shrubland to a grassland in the mesquite/mixed acacia savannas of south Texas.

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Response of C₃ and C₄ grasses to supplemental summer precipitation

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Abstract

Rangeland plant productivity and species composition are affected by moisture availability and grazing intensity. We examined warm- and cool-season grass productivity and relative distribution on grazed and ungrazed sites, receiving either natural precipitation or precipitation plus limited supplemental irrigation. The amount of additional water varied depending on rainfall during the previous week and was intended to shorten the interval between precipitation events and provide a more uniform seasonal moisture distribution. Irrigation treatments were superimposed in 1997 and 1998 on paddocks that had not been grazed for about 55 years or continuously stocked during the growing season for 15 years. Cool-season grasses dominated the ungrazed plots, comprising about 90% of the total biomass. In the grazed plots, the proportion of C₃ grasses ranged from 30 to 81%. The proportion of C₃ grasses in the grazed treatment decreased from spring to fall and decreased with supplemental irrigation. Root biomass was greater and more concentrated near the soil surface in the grazed compared with the ungrazed plots. Irrigation had no effect on root biomass in the grazed plots while irrigation reduced total root biomass and root biomass in the top 5 cm of the soil profile in the ungrazed plots. Irrigation increased total aboveground biomass only at the August 1997 harvest. Aboveground biomass of warm-season grasses, however, increased under irrigation in the grazed plots in August and November 1997 and August 1998. These increases, however, were offset by a reduction in cool-season grasses in November 1997 and August 1998. Warm-season grasses were particularly responsive to the supplemental irrigation treatments and tended to increase under irrigation at the expense of cool-season grasses. Because of the increased proportion of warm-season grasses, grazed plots were more responsive to irrigation than ungrazed plots.

Key Words: mixed-grass prairie, species composition, water stress

In mixed-grass prairies, the distribution of precipitation can be as important as the quantity received in determining forage productivity and the relative composition of species in the stand. The

Resumen

La productividad de las plantas del pastizal y la composición de especies son afectadas por la disponibilidad de humedad y la intensidad de apacentamiento. Examinamos la productividad de zacates de estación fría y caliente y su distribución relativa en sitios apacentados y no apacentados, recibiendo precipitación natural o precipitación mas irrigación suplementaria limitada. La cantidad de agua adicional varió dependiendo de la precipitación ocurrida durante la semana previa y se intento acortar el intervalo entre los eventos de precipitación para proveer una distribución estacional de la humedad más uniforme. Los tratamientos de irrigación fueron impuestos en 1997 y 1998 en potreros que no habían sido apacentados por aproximadamente 55 años o utilizados continuamente por 15 años durante la estación de crecimiento. Los zacates de estación fría dominaron en los potreros sin apacentamiento, comprendiendo aproximadamente el 90% de la biomasa total. En los potreros apacentados la proporción de zacates C₃ vario de 30 a 81%. La proporción de zacates C₃ en los potreros apacentados disminuyó de primavera a otoño y con la irrigación suplementaria. La biomasa de raíz fue mayor y más concentrada cerca de la superficie del suelo en las parcelas apacentadas en comparación con las no apacentadas. La irrigación no tuvo efecto en la biomasa de raíz de los potreros apacentados mientras que en los potreros apacentados la irrigación redujo la biomasa total de raíz y la biomasa de raíz en los 5 primeros centímetros del perfil del suelo. La irrigación incremento la biomasa total aérea solo en la cosecha de agosto de 1997. Sin embargo, en los potreros apacentados, la irrigación aumento la biomasa aérea de los zacates de estación caliente durante agosto y noviembre de 1997 y agosto de 1998, pero este aumento fue anulado por una reducción de los zacates de estación fría en noviembre de 1997 y agosto de 1998. Los zacates de estación caliente respondieron a los tratamientos de irrigación suplementaria y tendieron a incrementarse bajo irrigación a expensas de los zacates de estación fría. Debido a la mayor proporción de zacates de estación caliente, las parcelas apacentadas respondieron mejor a la irrigación que los potreros sin apacentamiento.

majority of annual precipitation occurs during the growing season (May to September), primarily as irregularly spaced thunderstorms. Between these periodic rainfall events, severe moisture stress can develop (Chung and Trlica 1980). Warm-season grasses are particularly dependent on summer precipitation while most cool-season grass growth occurs early in the season and is more

The authors wish to thank Matt Mortenson for his help in collecting the soil cores and Cathy Krumwiede for obtaining the soil moisture data.

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dependent on stored soil moisture (Hyder et al. 1976, Hart et al. 1993). The warm-season grass, blue grama (*Bouteloua gracilis* [H.B.K.] Lag. Ex Steud.), is particularly responsive to small summer rainstorms, and it has been proposed that the dominance of this grass in the Central and Southern Great Plains of the United States is related to its ability to utilize small volume rainfall events (Sala and Lauenroth 1982). Intensive grazing may reduce the negative effect of drought by reducing transpiring leaf area, thereby conserving soil moisture (Archer and Detling 1986, Day and Detling 1994). The effects of grazing intensity on plant responses to drought are species specific (Olson et al. 1985), suggesting that the interaction between drought and grazing could significantly affect botanical composition of rangelands.

Our objective was to determine the productivity and relative distribution of warm- and cool-season grasses on grazed and ungrazed sites that received either natural precipitation or precipitation plus limited supplemental irrigation. We hypothesized that additional moisture would favor production of warm-season grasses at the expense of cool-season grasses because of the greater ability of warm-season grasses to respond to summer precipitation. We also hypothesized that ungrazed plots would be more susceptible to drought than the grazed plots because of their greater leaf area, and thus, more responsive to supplemental irrigation.

Materials and Methods

The research was conducted at the High Plains Grassland Research Station near Cheyenne, Wyoming (41°11' N latitude, 104°53' W longitude) on a native mixed-grass rangeland. The climate is semi-arid with an annual frost-free period of 127 days and average annual precipitation of 384 mm. Precipitation is lowest in January, increases to a peak in late-May or early-June, then declines throughout the rest of the year. This decline is interrupted by a brief rainy period from mid-July to early-August.

Treatment pastures were established in 1982. Prior to establishment of the pastures, the area had not been grazed by domestic livestock for at least 40 years. This study was superimposed on 2 of 7 grazing treatments that exist at the site. They were, 1) ungrazed exclosures, and 2) pastures with continuous season-long stocking at a rate of 0.56 steers/ha

designed to remove $\approx 50\%$ of annual production. Both sites were located on an Ascalon sandy loam soil (mixed mesic, aridic argiustoll). This is a deep, well drained soil on nearly level alluvial fans. Yearly forage production ranges from about 800 to 2,100 kg ha⁻¹.

In the spring of 1997, two sub-sites dominated by grasses were selected within the grazed and ungrazed sites and 6 plots measuring 1.1 x 1.9 m were staked out within each sub-site. Non-grass species comprised about 30% of the aboveground biomass and did not differ significantly between grazed and ungrazed sites. Sub-sites within the grazed site were fenced for the duration of the experiment to protect them from grazing and to allow measurement of plant biomass production. All further reference to the "grazed site", therefore, refers to its historical use and not to management practices during the course of the experiment. Three plots per sub-site received supplemental irrigation while 3 received only ambient rainfall. Supplemental irrigation was applied from early-June through late-September in 1997 and 1998. Irrigation applications were designed to ensure that plots received water at rates equal to at least 17.5 mm week⁻¹. This rate was equal to average weekly precipitation rates during May, which is the wettest month of the year. Irrigation applications were designed to even out water availability throughout the summer. Using a hand-held hose and sprinkler nozzle attached to a 300 liter tank, water was applied weekly based on precipitation received during the preceding week. If rainfall during the week exceeded 17.5 mm then no additional water was added. If rainfall was <17.5 mm then sufficient water was applied to bring the total up to that amount.

Biomass was estimated in mid-May, early-August, and early-November in 1997 and 1998 by removing 10-cm diameter soil cores to a depth of 30 cm from each plot. Standing aboveground vegetation was separated into warm-season grasses, cool-season grasses and non-grass species. Blue grama and western wheatgrass [*Pascopyrum smithii* [Rydb.] A. Love (formerly *Agropyron smithii*)] were the predominant warm- and cool-season grasses, respectively, at both sites. Root, crown and litter fractions were collected but not identified by functional group. Roots were separated into 0 to 5, 5 to 15, and 15 to 30 cm depths. Roots were ashed to correct for any soil contamination of the washed root samples and root data are presented on an ash-free dry matter basis.

Gravimetric soil moisture content was determined from separate cores collected at the same time and adjacent to those used for biomass determinations.

The grazed plots were mowed after the August sampling in 1997 to simulate the grazing that would have occurred if the plots had not been fenced. Because biomass removed by mowing would have been present at the November sampling if it had not been removed, it was added to plant material collected at that time. Analysis of variance tests were conducted with years and grazing treatments as fixed and water applications as random effects. Fisher's protected least significant difference tests were used for means comparisons.

Results

Total precipitation in 1997 was 579 mm, exceeding the average annual precipitation of 388 mm by nearly 50%. Total precipitation in 1998, however, was 315 mm, or 81% of normal. Summer precipitation patterns were similar to annual amounts with the summer of 1997 (1 June to 30 September) being the 3rd wettest in the 82 years that records are available, while the summer of 1998 was the 7th driest. Despite the high rainfall in 1997, no rain fell during a 1 month period from late-June to late-July (Fig. 1). Another relatively dry period occurred between mid-August and mid-September. These 2 dry periods were separated by a month which received approximately 3-times the normal rainfall. Ten irrigations were applied in 1997, supplying 145 mm of supplemental water. The summer of 1998 was dry throughout the late-June to September period (Fig. 1), although April and May precipitation was slightly above normal (data not shown). In 1998, plots received 221 mm of additional moisture in 16 irrigations.

Both irrigation treatment and previous grazing management had little effect of soil moisture in 1997 (Fig. 2). Because of the abundant rainfall just before the August harvest and again in late September (Fig. 1), soil moisture in the cores was near field capacity in all plots when the last 2 harvests were taken in 1997. Because soil moisture measurements were only collected at the time of harvest, we have no data on how irrigation treatments might have affected soil moisture prior to the late July and early August rains. Significant soil moisture deficits developed during the summer of 1998 with the ungrazed plots being wetter than the grazed plots (Fig. 2). Irrigation treat-

Fig. 1. Weekly precipitation and irrigation applications during the summers of 1997 and 1998. When precipitation for the proceeding week was less than 17.5 mm supplemental irrigation was applied to bring the weekly total to 17.5 mm.

ments significantly ($P < 0.01$) increased soil moisture content at the August harvest in both the grazed and ungrazed plots. Soil moisture was again near field capacity in all plots when harvests were taken in November 1998.

Supplemental irrigation had no significant effect on root biomass in the grazed plots (Table 1). In the ungrazed treatment, irrigation reduced total root biomass and the biomass of roots in the top 5 cm of the soil profile. Grazed plots had significantly larger root systems than the ungrazed plots and a greater proportion of the roots were located near the soil surface in the grazed plots. Seventy nine percent of the roots in the grazed treatment were in the top 5 cm compared with 69% in the ungrazed plots. Irrigation treatment had no detectable effect on root distribution within the soil profile.

Supplemental irrigation increased aboveground biomass (C_3 plus C_4 grasses) at the August sampling in 1997 but not in 1998 (Fig. 3). There was no difference in aboveground biomass between the August 1997 and August 1998 harvests in the non-irrigated treatment. However,

November aboveground biomass in 1998 was significantly lower than in November 1997, and significantly lower than the August 1998 harvest, suggesting that senescence and transfer of leaves to the litter pool was proceeding faster than leaf growth. Adding supplemental water did not enhance total late-summer biomass production compared with the non-irrigated plots.

The ungrazed site was dominated by C_3 grasses (Fig. 4 and Fig. 5) in both years and at all 3 harvests within each year. Irrigation increased the biomass of C_3 grasses in the ungrazed plots at the August

1997 harvest, but had no effect on C_3 grasses at any other harvest. Irrigation had no effect on C_3 biomass at any harvest in the grazed plots. However, irrigation increased biomass of C_4 grasses in the grazed plots at the August and November 1997 harvests ($P < 0.05$). A similar trend of increased biomass production with irrigation was observed for C_4 grasses in the grazed plots in August 1998 ($P < 0.10$). Increased production of C_4 grasses occurred in both the irrigated and non-irrigated grazed plots following mid-summer rains in 1997. C_3 grasses did not respond to the above normal rainfall in 1997 in either grazing treatment.

The ungrazed sites had a much greater proportion of C_3 grasses than the grazed sites. When all harvests were combined, C_3 species accounted for 92% of all grasses in the ungrazed plots (Fig. 5). Irrigation caused a decrease in the proportion of C_3 grasses in the grazed plots. When all harvests were combined at the grazed site, the percentage of C_3 grasses decreased from 63% in the non-irrigated to 52% in the irrigated treatment ($P < 0.05$). Averaged across years, the percentage of C_3 grasses at the grazed site decreased with successive harvests, falling from 66% in May to 48% in November ($P < 0.01$). This decrease was much more pronounced in 1997 when mid-summer rainfall led to an increase in late-summer C_4 grass production.

Discussion

We hypothesized that supplemental irrigation would favor the production of warm-season grasses at the expense of cool-season species because of the greater ability of warm-season grasses to respond to summer precipitation. We also hypothesized that ungrazed plots would be more susceptible to drought than the grazed plots because of their greater leaf area, and thus, would be more responsive to supplemental irrigation.

Our data supported the hypothesis that

Table 1. Root biomass response to irrigation and previous grazing regime at the High Plains Grassland Research Station near Cheyenne, Wyo. Data are averaged across harvests and years with the exception of the May 1998 data which are missing. Data are expressed per m^2 of soil surface area to facilitate comparisons with aboveground biomass and are ± 1 Standard Error.

Treatment	Soil Depth			Total Roots
	0–5 cm	5–15 cm	15–30 cm	
	(g m ⁻²)			
Grazed/non-irrigated	1037 ± 87	171 ± 14	82 ± 9	1296 ± 88
Grazed/irrigated	1035 ± 101	188 ± 23	90 ± 13	1312 ± 95
Non-grazed/non-irrigated	652 ± 48	146 ± 20	122 ± 22	921 ± 53
Non-grazed/irrigated	551 ± 26	162 ± 22	104 ± 16	816 ± 35

Fig. 2. Soil moisture content under plots that received only natural precipitation or that received weekly supplemental irrigation applications when needed during the summer to bring the weekly total to at least 17.5 mm.

Fig. 3. Effect of irrigation on total grass production (C_3 plus C_4) at mixed-grass prairie site near Cheyenne, Wyo. Data are combined across grazing treatments which showed no significant difference in total grass production.

C_4 grasses are more responsive than C_3 grasses to small precipitation events. Supplemental irrigation reduced the proportion of C_3 grasses in the grazed plots in 1997 and 1998 and in the ungrazed plots in 1998 (Fig. 5). In addition, when data were averaged across years, grazing treatments, and harvests, C_4 biomass increased under irrigation ($P = 0.02$) while C_3 biomass was unaffected. Chung and Trilca (1980) found that blue grama sods were capable of rapid recovery upon the relief of soil water stress to -1.5 MPa and suggested that blue grama was adapted to habitats where periods of extreme drought alternate with periods of abundant water. Sala and Lauenroth (1982) reported that leaf water potential and leaf conductance

to water in blue grama increased within 12 hours following a small (5 mm) precipitation event, and that improved leaf water relations lasted for up to 2 days. This rapid response to rainfall would allow blue grama to be highly competitive under fluctuating moisture conditions.

In the current study, warm-season grass biomass in August and November 1998 was 78% greater in the irrigated compared with the non-irrigated plots (Fig. 4), while cool-season grass biomass decreased under irrigation by 12% during the same period.

Blue grama has a dense, shallow root system (Bartos and Sims 1974, Schuman et al. 1999) improving its access to moisture received from irrigation or summer rainstorms. Western wheatgrass, however, has a relatively deep root system that is more suitable for accessing moisture stored in the soil profile during winter and early spring. These differences in root architecture were evident when root systems from grazed and ungrazed plots were compared (Table 1). The grazed plots, which had a greater proportion of warm-season grasses than the ungrazed plots, not only had greater total root biomass but roots were concentrated nearer the soil surface. In the grazed plots, 79% of the roots were in the top 5 cm of the soil profile compared with 69% in the ungrazed plots.

Climate, particularly water availability, is thought to be the primary determinant of species composition with other factors such as grazing operating within the constraints imposed by moisture conditions (Milchunas and Lauenroth 1993, Dormaar et al. 1997, Biondini et al. 1998, Stohlgren et al. 1999). Olson et al. (1985) suggested, however, that each species reacts to precipitation and grazing in a unique manner. Grazing often results in a shift in composition from tall to short species, and in selection for prostrate growth forms within a species (McNaughton 1983, 1984), producing a greater uniformity in the horizontal distribution of biomass than is found on non-grazed sites (Milchunas and Lauenroth 1989). Schuman et al. (1999) found that heavy grazing resulted in an increase in blue grama and a decrease in western wheatgrass when compared with a light grazing treatment.

Resistance of blue grama to grazing has been related to its ability to maintain a

Table 2. Mean daily air temperature and total monthly evaporative demand during the growing season at the High Plains Grassland Research Station near Cheyenne, Wyo.

	May	June	July	August	September	October
-----Air Temperature (°C)-----						
1997	9.7	15.5	18.1	16.9	15.5	7.5
1998	10.6	12.3	19.6	18.4	16.1	7.7
82 yr. Average	10.7	16.2	20.1	19.2	14.3	8.2
-----Pan Evaporation (mm)-----						
1997	90	96	91	47	71	78
1998	71	54	195	133	150	133

Fig. 4. Effect of irrigation on C₃ and C₄ grass production on sites that had not been grazed for about 55 years (ungrazed) or had experienced 15 years of continuous grazing (grazed).

vigorous root system and high carbohydrate reserve levels after defoliation (Buwai and Trlica 1977). Because defoliation is usually less damaging to blue grama than to western wheatgrass, blue grama often increases as stocking rate increases while western wheatgrass decreases (Hart et al. 1993). The lower proportion of C₃ grasses that we observed in the grazed plots was consistent with these observations. In the ungrazed plots, species composition remained more constant across years, harvests and irrigation treatments than in the grazed plots, suggesting that the grass community had become a relatively stable, C₃ dominated system in the 50 plus years that grazing had been excluded from those sites. Fifteen years of grazing, however, produced a more dynamic system with species composition being affected by irrigation treatment, harvest, and year by harvest interactions.

Even though yearly precipitation was 84% greater, and June to September precipitation 178% greater in 1997 than 1998, May and August biomass in non-irrigated plots were similar in 1997 and 1998 (Fig.

3). Only in November was biomass in non-irrigated plots greater in 1997 than in 1998. Others have found that forage yields are not necessarily related to yearly mois-

ture availability (Wilms et al. 1993, Heitschmidt et al. 1999). To understand the apparent discrepancies between forage production and precipitation, seasonal trends in the growth of the different plant functional groups must be compared with seasonal changes in rainfall and evaporative demand. Cool-season grasses, in general, and western wheatgrass, in particular, grow primarily during the spring and early-summer. In an earlier study at the same site, western wheatgrass produced little growth in either grazed or ungrazed plots after mid-July (Hart et al. 1993). Blue grama, on the other hand, continued to grow through August (Hart et al. 1993) and depended on summer precipitation to prevent tiller death and thinning of the stand (Hyder et al. 1976).

The early summer of 1998 was characterized by adequate precipitation in April and May, lower than average temperatures in May and June and a concomitant reduction in evaporative demand compared with the same period in 1997 (Table 2). Under these conditions, both C₃ and C₄ biomass production in 1998 were equal to production in 1997. In a Canadian study involving many of the same species found on our sites, high precipitation and low pan evaporation during the spring of an otherwise dry year resulted in greater herbage production than was observed in years with average precipitation but with less favorable seasonal distribution patterns (Wilms et al. 1993). The severe drought that developed in July, August, and September 1998 severely inhibited late-summer C₄ production compared with 1997 when abundant mid-summer rainfall produced a flush of late-summer growth (Fig. 4).

Fig. 5. Effect of irrigation on the proportion of C₃ compared with C₄ grasses on sites that had not been grazed for about 55 years (UG) or had experienced 15 years of continuous grazing (GR).

Our data did not support the second hypothesis that ungrazed plots would be more susceptible to drought because of their increased leaf area and greater evapotranspiration. During the greatest period of drought in August 1998, soil water content was actually greater in the ungrazed plots (Fig. 2). The taller plants in the ungrazed plots could have shaded the soil surface, reducing evaporation. In August, 61% of the cool-season grass standing biomass was living compared with 75% of the warm-season grass biomass. The lower proportion of green living tissue could have also resulted in reduced transpiration in the C_3 dominated ungrazed plots. LeCain et al. (2000) also found that soil water content was greater in ungrazed compared with grazed plots and suggested that the greater accumulation of litter and standing dead in the ungrazed plots acted as a mulch, conserving moisture stored during the winter. The ungrazed plots were also less responsive to supplemental irrigation because they contained only a small proportion of the C_4 grasses that were most responsive to additional summer moisture availability.

In conclusion, supplemental irrigation increased warm-season grass production relative to the production of cool-season grasses. The shift toward warm-season grasses probably occurred because of the larger, more shallow root systems of the warm-season grasses which improved moisture acquisition following irrigation treatments. Contrary to our original hypothesis, there was no indication that ungrazed plots were more sensitive than grazed plots to drought stress, or more responsive to supplemental irrigation. This was probably because of the mulching effect of the litter and standing dead and because of the dominance of deep-rooted cool-season species in the ungrazed plots.

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Book Reviews

The New Economy of Nature: The Quest to Make Conservation. By Gretchen C. Daily and Katherine Ellison. 2002. Island Press. 260 pp. US\$25.00 hardcover. ISBN 1-55963-905-8.

Landowners, take heart. If you are resigned to the idea that real ecological management subtracts from your thin bottom line, this book offers a glimpse of a different balance sheet. Resource managers, don't give up. A different gauge may soon measure your best efforts.

Sound too dramatic? Perhaps, perhaps not. There are fresh ideas presented here, ideas that tear at the tired fabric of the status quo.

Author Dr. Gretchen C. Daily is an accomplished interdisciplinary research scientist at Stanford University's Department of Biological Science. Katherine Ellison, currently a consulting writer at Stanford's Center for Conservation Biology, has spent more than 20 years as an international journalist and earned a Pulitzer Prize along the way. The examples they have chosen for *The New Economy of Nature* reflect diverse efforts around the world to establish economic values for natural values, for a watershed's ability to provide clean water, for unfragmented wildlife habitat, and for the biological diversity of a rainforest.

New York City's drinking water, provided by the upstate watershed for over 150 years, has long been envied for its taste and purity. By the 1990's, however, the city faced the choice between a multi-billion dollar filtration system and a watershed enhancement approach costing perhaps one-fourth as much. The city is currently implementing the watershed approach with some genuine successes, although not yet with total success. One problem is that the cost of the natural approach has gone up while the cost of the technology approach may be coming down; the purely economic argument favoring one over the other is less clear. Another is that the pace of the implementation may not be quick enough to satisfy the regulatory agencies involved. Last but not least, the extremist groups at either end of the spectrum, those who are all for the environment and those who are all for property rights, have staked out their positions in the courts. The authors do a nice job of pointing out the problems along with the triumphs in this story, and they provide the same balance in most of the others.

Urban sprawl is the plotline and King County, Washington is the setting for another story. Characters include environmental groups, developers, and big business, but the leading role goes to county political leader Ron Sims. With Seattle as its seat, the population of King County rose by 44 percent between 1980 and 1998. Much of this growth has been fueled by wealth, and the urge to carve up large chunks of the forest into 40-acre parcels has proven hard to resist. The twin pressures of population growth and land degradation are, in the words of the authors, "in real time". Ron Sims has used a rare blend of idealism, political savvy, and pragmatic compromise to engineer several innovative successes. One success has been the creation of a market in transferable development rights (TDR's), where rural development rights have been purchased and shifted to urban areas. Part of this shift has been accomplished using the Endangered Species Act and the recently listed chinook salmon; local governments with jurisdiction over salmon habitat risk sanctions or lawsuits for failing to protect the habitat. This approach has had the effect of establishing a market value for healthy habitat, and King County

has had at least some success using federal funds to limit growth in some areas, and channel it into others.

Many of the stories in this book revolve around people invited to take part in the Kaloomba group brainstorming sessions, named after the group's first meeting place in Australia in 1999. The authors pick their stories well to reflect the diverse backgrounds and opinions of the people involved—biologists and foresters, venture capitalists and mutual fund managers, among others, share the spotlight at different times. The focus is international and places like Costa Rica and Australia figure prominently. Regardless of location, however, there is a pattern. The authors conclude that every project in the book has three things in common: unconventional and creative thinking, an understanding of the implications of each option, and a comparison of the tangible and the intangible assets of each option. They make a strong case that viewing nature's services this way can revolutionize conservation work.

A couple of other conclusions come through less clearly in the writing, and perhaps the authors should have given a little more space to them. Any potential land use must have some kind of economic value or it will not be valued by society. Land uses that are mutually exclusive must also be at least roughly equal in value, or the chosen use is a foregone conclusion.

Another conclusion became apparent as I read further, one I'm not sure the authors intended; no single ecological benefit, by itself, has sufficient economic clout to carry the day. Just as the single-minded protection of one endangered species cannot ultimately succeed, so too will the economy of nature ultimately fail if each benefit is weighed separately.

If you enjoy looking at resource issues from fresh perspectives, this book will be worthwhile reading. It will challenge certain assumptions you may hold, regardless of the view you start from. It seems appropriate to finish by borrowing from the book a quotation of Albert Einstein used to begin a chapter: "No problem can be solved from the same consciousness that created it."—*Art Meen*, USDA-Natural Resources Conservation Service, Fredonia, Arizona.

Human Well-Being and the Natural Environment. By Partha Dasgupta. 2001. Oxford University Press, Oxford, UK. 305p. US\$35.00 hardbound. ISBN 0-19-924788-9.

Is it certainly true that most extant measures of the quality of life pay little or no attention to the natural environment. Partha Dasgupta finds this to be a rather disquieting state of affairs. Consequently, his objective in this book is to expansively explore alternate ways of constructing quality of life indices that incorporate the natural environment into them. The book contains 15 chapters and a technical appendix; the chapters themselves are divided into 5 parts. In the remainder of this review, I shall attempt to give the reader a flavor for the intellectual contributions of this book by selectively sampling from each of the 5 parts.

Part I consists of 3 chapters and this part generally explains the meaning of valuation and evaluation. The individual chapters here discuss the notion of well-being, how alternate social states may be ordered, and why it is salient to measure human well-being. In particular, it is pointed out that wealth and discounted social profit are linear in quantities; moreover, they are useful measures of social well-being because they "reflect social well-

being, in that they correlate with it" (p. 31). There is one quixotic sentence here that deserves some comment. While discussing imitation and the demonstration effect, the author says that it "has proven hard to obtain direct evidence of imitative behaviour. So there isn't much of it" (p. 39). It isn't obvious to me that just because one cannot find *direct* evidence of a phenomenon, it necessarily follows that this phenomenon doesn't exist.

The focus of Part II is on the measurement of current well-being. Chapter 4 focuses on the notion of citizenship and Chapter 5 marshals available data to make the valuable point that civil liberties and democracy are not only inherently worthwhile but that they are also likely to be useful in generating material progress in the poor nations of the world. Although this is a useful point, the author's prose elsewhere in this part leaves me unsure as to what he thinks about the true worth of GNP as a measure of current well-being. He first points out (on p. 56) that contemporary data imply that GNP is *not* a "wildly misleading" measure of present well-being. Then, a little later (on p. 62), he questions whether a "general moral" can be drawn from his exercises which suggest that GNP is *not* a "vastly misleading" measure of current well-being. Then, there is a rather odd error. On p. 82, the author says that "GNP (in a closed economy) is the sum of aggregate consumption and gross investment." This is not true. What is true is that in a closed economy, GNP is the sum of aggregate consumption, gross investment, *and* government purchases.

The subject matter of Part III is the measurement of intertemporal well being. Without a doubt, this is the finest part of this book. Specifically, Chapter 8 contains an excellent account of the ways in which ecological matters influence the estimation of accounting prices. In this chapter, the author rightly points out that biodiversity plays a role in making ecosystems resilient to alterations in the conditions they experience that "species abundance in ecosystems is like spare capacity: it offers an insurance device for ecosystems" (p. 129).

Although Part III in general is undeniably a contribution to the extant literature, two issues discussed here are unclear. The first issue concerns the relevance of the very long run or the distant future in economic analysis. On p. 98, the author argues that the Koopmans formulation should not be rejected because it recommends a decline in consumption in the "distant future." This suggests that what happens in the very long run is *not* particularly relevant. But then the author justifies his "constant population size" assumption by saying that "changes in the size of the population when averaged over time will be zero over the very long run" (p. 98). Clearly, for this assumption to be valid, what happens in the "very long run" is most relevant. The second issue pertains to the usefulness of exercises that attempt to test theories. For instance, there now exists a sizeable literature that has documented the repeated experimental violations of the predictions of expected utility theory. Although this should cause us to think seriously about the validity of expected utility theory, the author doesn't think so. As he puts it, "[t]hat the choices we make in the laboratory don't conform to expected utility theory doesn't mean that the theory is not the correct ethical basis for valuing and evaluating" (p. 101).

How should policies be evaluated in imperfect economies? This question is ably addressed by the 3 chapters in Part IV. The author first asks us to view policy changes as perturbations and then he tells us that a particular policy should be undertaken only if it adds to wealth. Chapter 11, in particular, contains an erudite discussion of the manner in which the consumption rate of interest can be derived from macroeconomic forecasts. As the author perceptively points out, "social discount rates in consumption

numeraire are not a primary ethical concept: they are derived jointly from an overall conception of social well-being and the economic forecast" (p. 182). For the most part, this is a perspicacious chapter, even so, the author's belittling of Martin Weitzman's recent research on the concept of gamma discounting is likely to leave a bad taste in the mouth of many readers.

The 3 chapters of the concluding Part V focus on the valuation of potential lives. The author tells us that it is necessary to value potential lives because recent advances in genetics have made it possible for policies to "affect the quality of people who will be born" (p. 207). Finding problems with both average and classical utilitarianism, the author asks us to pay close attention to "generation-relative utilitarianism." Why? this is because-relative utilitarianism "prescribes neither a very large population nor a very small population. Instead, it offers a wide space in between, within which more detailed ethical considerations can be embedded" (p. 228). The issues discussed by the author in this part of the book are complicated and, to a large extent essentially philosophical in nature. Consequently, the author deserves praise for entering and then attempting to chart a course in relatively uncharted terrain. Having said this, it should also be noted that it is certainly possible to disagree with a number of the author's claims and interpretations. For instance, on p. 229 the author says that "[m]ortality threatens to render the achievements of our life transitory, and this threat is removed by procreation." It seems to me that mortality can also have the opposite effect, i.e., it can magnify one's achievements in a way that the state of being alive cannot. Moreover, even if the author's contention in the first part of the above quoted sentence is true, it is not at all obvious that the hypothesized "treat" is indeed removed by procreation. In fact, one could credibly claim that most people procreate at an age in which they typically have few "achievements" that they would effectively like to perpetuate.

The subject matter of this book is undeniably salient and the author has many interesting and perceptive things to say about this subject matter. Even so, the author's occasionally hectoring style and his perplexing habit of repeatedly using double negatives (see, for instance, p. 50, 92, 117, 135, 146, 209) tend to diminish the salience of the many useful points that he makes. In conclusion let me say that although it is not possible to heap unqualified praise on this book, it is certainly very good in parts. Consequently, a perusal of those parts should provide the reader with a nuanced understanding of the many ways in which the natural environment affects human well-being.—*Amirajeet A. Batabyal*, Rochester Institute of Technology, Rochester, New York.

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