A Forage Allocation Model for Four Ungulate Species in Theodore Roosevelt National Park

by

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Introduction

Today, natural resource managers are faced with a confusing array of resource-related decisions on the distribution and optimization of scarce resources. This, together with the growing movement to restore fragmented ecosystems, has taxed the limitations of many resource agencies. An ongoing attempt has been made in Theodore Roosevelt National Park (TRNP) to restore extirpated fauna and preserve historical resources. Pronghorn (Antilocapra americana), bison (Bison bison), and California bighorn sheep (Ovis canadensis california) were reintroduced into the South Unit (SU) of TRNP in 1951, 1956, and 1959, respectively. Feral horses, from a variety of sources, have established themselves in the Park, and are now considered a historical resource. An elk (Cervus elaphus) reintroduction in 1985, together with resident mule deer (Odocoileus hemionus) and white-tailed deer (O. virginianus) completed the historic ungulate assemblage in the badlands ecosystem (TRNP 1984).

Although one of the major management goals in TRNP is to maintain plant and animal communities in conditions as close to those of the early 19th century as possible (TRNP 1984), this goal is not feasible within the spatial constraints imposed by the Park boundaries without management. Managing mixed ungulate communities at levels consistent with maintaining healthy native plant communities can be facilitated by use of a computer model which allows managers to assess the likely consequences of carrying specific numbers of each ungulate species within the Park.

We developed a linear model for the allocation of forage resources to ungulates in Theodore Roosevelt National Park. Our model was limited to forage allocation among 4 most numerous and wide-ranging species in the Park: mule deer, bison, elk, and feral horses and was based on spring-summer dietary demands. The model was deterministic in that the value of state variables was determined in accordance with "known" biological and physical relationships with no randomly varying elements (Smith and Williams 1973).

Methods

Forage Allocation Model Structure

The forage allocation model selected for Theodore Roosevelt National Park incorporates a deterministic, linear programming (LP) framework. Linear programming is the process of simultaneously solving a series of linear algorithms. The model utilizes a linear programming function in Quattro Pro (Borland Internat. Inc., 1989), a menu-driven spreadsheet, database, and graphics program. The model is structured so that 4 decision variables (ungulate species: elk, bison, feral horses, and mule deer) maximize use of the constraints (allowable forage offtake) within the constraints of state variables (body size, diet selection, production, intake, herd composition). Pronghorn and white-tailed deer also occurred at TRNP, but these species had limited densities and distributions and were not considered in the model.

The Quattro Pro algorithm uses the revised simplex technique or primal-dual problem technique. An objective function is formulated which defines how the resource (forage) will be efficiently allocated among the competing decision variables (the ungulates). The objective function is then solved within the constraints (forage available) arriving at an optimal solution (number of ungulates) from an infinite number of feasible (suboptimal) solutions. The optimal solution for the objective function is the optimal mix of the maximum number of decision variables that completely utilizes the most limiting constraint or driving variable, without overutilizing it. The optimal solution can be conceptualized as the most extreme of all vertices in the solution space which maximize the objective function. The solution represents the sum of individual decision variables multiplied by their coefficients.

Assumptions

Inherent within the forage allocation model are certain assumptions which, if violated, invalidate the model and the resultant outcome. The manager should be aware of these assumptions and how they effect the formulation of an optimal solution.

1. Certainty - The model is organized in a deterministic fashion, meaning that values reported for variables are point estimates and have no variance associated with them. Values we used were based on mean values of samples. For instance, live weights and intake were values reported from the literature from studies with varying sample sizes; diet selection was based on large sample sizes over several seasons; and, vegetative production estimates were average values over several growing seasons.

2. Linearity - This assumes that the function of driving variables (e.g. forage consumed) is linear.

3. Nonnegativity - Implies that all decision variables ("X's" or ungulate species) must be ≥ 0 in the objective function.

4. Additivity - Suggests that the contribution of each decision variable (ungulate) to the objective function is mutually exclusive and is not affected by the contribution of other ungulates whether they are considered separately or together. Also, grazing by 1 ungulate species is considered to be unaffected by their own population size or the population size or behavior of another ungulate species.

Formulation

The objective is to optimize numbers and species of herbivores so that forage consumption is maximized and forage remaining after grazing is minimized. The problem is formulated algebraically through a series of algorithms:

The objective function which will be solved takes the form of:

$$\text{MAX} \sum_{j=1}^{4} X_j$$

where: X_j = Decision Variables (ungulate species, such as X_1=elk; X_2=bison; X_3=mule deer; and X_4=feral horses).

By expansion the formula becomes:

$$Z = 1X_j \quad \text{or} \quad Z = 1X_1 + 1X_2 + 1X_3 + 1X_4$$

where: Z = The solution to the objective function (total number of ungulates).
1 = Objective Function Coefficient (may be a value other than 1).

The objective function is subject to constraints which take the form of the inequality:

$$\sum_{j=1}^{4} D_{ij} R_j X_j \leq H A_i U_i$$

where: Linear Constraint Coefficients:
D_{ij} = proportion of the ith plant species or forage group grazed by the jth animal species.
R_j = daily consumption of the jth ungulate species.

Constant Constraint Terms (or RHS - Right Hand Side):
H = size of grazing area.
A_i = availability of allowable herbage of the ith forage species (Production).
U_i = Allowable Use Factor (AUF) of the ith forage species

By expansion the constraints are:

$$(D_{1,1}\ T\ R_1) + (D_{1,2}\ T\ R_2) + \ldots \leq H\ A_1\ U_1$$
$$(D_{2,1}\ T\ R_1) + (D_{2,2}\ T\ R_2) + \ldots \leq H\ A_2\ U_2$$
$$(D_{3,1}\ T\ R_1) + (D_{3,2}\ T\ R_3) + \ldots \leq H\ A_3\ U_3$$
$$\text{etc.} + \text{etc.} + \ldots \leq \text{etc.}$$

where: T = grazing period

Alternatively, the constraints can be can be notated as (Norland 1986):

$$AX_1 + BX_2 + CX_3 + DX_4 \leq RHS$$

where: A, B, C, D = Coefficients of ungulate species representing the rate at which a typical animal will use a dietary item.
RHS = Right Hand Side - the amount of allowable forage found in the grazing area under investigation.

Model Inputs

Five major inputs were used in the model:

1. (H) - Hectares of each Habitat Types (HT)/Mapping Units (MU)/ Complex within TRNP.
2. (A_i) - The production of the major dietary items within each HT/MU/Complex.
3. (U_i) - The percent allowable use of each dietary item.
4. (D_{ij}) - The diet (food habits) of each ungulate.
5. (R_j) - The average forage intake during the 6-month growing season for a typical animal of each ungulate species.

1. Vegetation Classification and Inventory - (H)

Numerous systems have been used to classify vegetation communities in and around TRNP (Hanson and Whitman 1938; Nelson 1961; Brown 1971; Redmann 1975; Whitman 1979; Hansen et al. 1980; Hansen et al. 1984; Marlow et al. 1984; Girard 1985; Hirsch 1985). In this study, we decided upon Marlow et al. (1984) because it: 1) had been applied to both grassland/shrubland communities and woodland communities; 2) had mapped all communities and calculated their hectarage for the SU of TRNP; 3) had measured or estimated vegetational production for most forage species in most communities.

The system employed by Marlow et al. (1984) (also used in Norland 1984; Sullivan et al. 1988; Westfall et al. 1989) categorized landforms and vegetational communities by 2 schemes - thereby creating 2 data layers for a 2-tiered manual geographic information system (GIS). The first scheme, Physiographic Types (PT) (called Physiographic Class in Marlow et al. 1984 and Norland 1984), classified large areas according to landform appearance, landform origin, and the gross structure of the associated vegetation (e.g. grassland, shrubland, wooded draw, etc.). These categories were further subdivided into smaller units, called Habitat Types (HT), creating the second mapping scheme. Habitat Types were based on the vegetational mapping system developed by Daubenmire (1952, 1968, 1970).

Daubenmire (1952) first developed a system of mapping discrete vegetational units based on potential climax vegetation (not existing vegetation) for forest types and later applied this to shrub-steppe vegetation of (Daubenmire 1970). Habitat Types were based on the premise that under certain climates, substrates and landforms, specific vegetational assemblages would eventually develop, identified as climax vegetation. Consequently, identification of these "Habitat Types" could be made from a combination of vegetation composition, soil types and/or landforms.

Other systems had been developed previous to Daubenmire (1952) which used the "discrete unit" approach to vegetational mapping. Dyksterhuis (1949, 1958) developed the concept of Range Sites, which also referred to potential rather than existing vegetation, for vegetation on the Great Plains. The Range Site concept has been used by a number of Federal Agencies, most notably the USDA Soil Conservation Service, to categorize rangeland and shrubland, but seldom used for woodland communities. The Soil Conservation Service in North Dakota developed criteria for Range Sites based on the level of departure from representative plant community (USDA Soil Conservation Service 1975). This level of departure, called Condition Classes, was measured by the relative percentage of vegetation classified as decreasers (most characteristic of climax vegetation), increasers and invaders.

For grassland/shrubland communities of western North Dakota the Range Sites of the SCS and Habitat Types of Marlow et al. (1984) may describe the same vegetational unit - differing in name only (eg. Agropyron smithii / Stipa comata HT). In fact, the Habitat Type system developed by Norland (1984) patterned many Habitat Types after Range Sites and used the estimate of vegetational production for some forage species and classes. Other Habitat Types were patterned after Whitman (1979), Hanson et al. (1980), Girard (1985), and Hirsch (1985).

Most areas of TRNP are relatively pristine and have been altered little by man; therefore, the Habitat Type classification scheme has direct management implication by describing not only potential but existing vegetation as well. However, some areas of the SU of TRNP have been extensively altered by anthropogenic or natural forces or are in the early stages of succession. These areas are unlikely to develop into climax vegetation within the management time-frame of the Park, and therefore, could not be categorized as Habitat Types. Such areas included grasslands previously overgrazed by livestock which have changed vegetational composition, campgrounds, and visitor centers, etc. These areas were called Mapping Units (MU). Disturbed vegetation units have been described previously in the literature. Daubenmire (1968) classified "anthropogenic disclimaxes" and Arno and Pfister (1977) called existing vegetation disturbed by man-made or natural forces "cover types."

In certain areas Habitat Types or Mapping Units were too small to map or too intermixed to differentiate - creating a Habitat Type mosaic. These areas were called Complexes and the proportion of Habitat Types which made up each Complex was calculated. Tables 1 and 2 includes the listing and definition of all PTs and HTs/MUs/Complexes in the SU of TRNP. The area of individual HTs/MUs/Complexes and their composition in each PT was measured from infrared aerial photographs (1 to 12,000 scale) obtained from the Bureau of Land Management by Marlow et al. (1984) and followed by intensive ground-truthing by Norland (1984).

Several habitat types were further subdivided into smaller habitat types, referred to as "estimated" habitat types, by Norland (1988). These are refinements of the original habitat typing done in TRNP by Norland (1984) and Marlow et al. (1984). The composition of the original habitat types of these new habitat types were determined by Norland (1988) and the hecterage of all habitat types was readjusted. For analytical purposes, the Park was divided into 9 geographical regions, and the area of each measured by Marlow et al. (1984). Table 3 includes a listing of all HTs/MUs/Complexes and their hectarage within these geographic regions.

Table 1. Description of Physiographic Types (PTs) in the SU of TRNP.

1. Bottom Grasslands: large flat grassed alluvial deposits found on high floodplains of the Little Missouri River and its larger tributaries.

2. Breaks: consists of areas noticeably devoid of vegetation, or if vegetation does exists, it is situated on steep slopes.

3. Sagebrush Bottoms: floodplains dominated by silver sagebrush (*Artemisia cana*) along with substantial grass cover.

4. Upland Grasslands: level to rolling grasslands found on plains above the river valley. These lands are typical of the Northern Great Plains.

5. Prairie Dog Towns: lands which have been or are being influenced by prairie dogs. At the edges of the towns plants are still characteristic of the former plant community. Nearer the center, vegetation is absent or dominated by unpalatable perennial plant species.

6. Ridge & Ravine: lands highly dissected by watercourses and covered by various grasses, shrubs, and trees.

7. Old River Terrace: level grasslands 200 to 500 feet above the river which are situated on terraces formed before rapid downcutting of the river.

8. Scoria Hills: lands influenced by scoria (a clinker formed from the baking of clays adjacent to burning coal veins) which produce differential weathering of the land. This weathering produces a very rugged topography which is covered by various grasses and shrubs.

Table 2. Description of Habitat Types (HT), Mapping Units (MU), and Complexes in the SU of TRNP.

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1. Agropyron smithii / Stipa viridula HT (WG)

Distinguished by the presence of Stipa viridula in habitats having heavy soil, protected from the wind, or extra moisture from runoff. Agropyron smithii is the primary grass component. Located on well drained, fine textured soils on terraces or gentle uplands with slopes of 0-4%.

2. Agropyron smithii / Stipa comata HT (WN):

Agropyron smithii is the major grass component. Bouteloua gracilis is the dominant short grass species. Shrubs are generally not found in this habitat type. Located on loamy to clay soils on uplands and flat terraces with slopes of 0-12%.

3. Agropyron smithii / Bouteloua gracilis / Distichlis spicata HT (CP):

Characterized by the presence of saline - sodic claypan with scattered bare spots devoid of vegetation. Located on level or hummocky terrain with slopes of 0-6%. Soils have a surface of loamy topsoil with a clay layer 0-25cm below this.

4. Stipa comata / Bouteloua gracilis HT (SC):

Canopy cover is dominated by Stipa comata; however, Bouteloua gracilis and Carex spp. contribute substantially to relative basal coverage. Located on gently rolling slopes dominated by sandy uplands with sandy loam or clay loam in the uppermost soil layer.

5. Schizachirium scoparium HT (L):

Schizachirium scoparium occurs in bunches and is the primary grass component. Located on moderate steep to steep upland on north, northeast and western exposures with slopes from 18-20%. Soils are shallow, unleached clay loams to sandy loams.

6. Schizachirium scoparium / Juniperus horizontalis HT (J):

Vegetation is sparse with soil and exposed rock comprising up to 64% of total coverage. Shrubs are common. Located on hilltops and buttes with very shallow loamy soils and slopes ranging from 20-24%.

7. Artemisia tridentata / Atriplex confertifolia HT (S):

Vegetation is sparse, comprised mostly of low shrubs. Located where barren outcroppings of bentonite clay and/or lignite deposits were obvious. Soils poorly developed and range from silty clay loam to clay loam.

Table 2. Continued.

8. Artemisia tridentata / Bouteloua gracilis HT (BS):

Artemisia tridentata abundant above a heavy grass cover comprised mostly of Bouteloua gracilis and Agropyron smithii. Located on upper slopes and stream terraces having shallow, fine textured soils and slopes ranging from 2-20%.

9. Artemisia cana HT (AA):

Dominated by Artemisia cana, but Symphoricarpos occidentalis frequently also occurs there. Found on flood plains and low terraces. Frequently occupies large flats along streams and creeks. Soils vary due to periodic flooding and new depositions being laid down. Textures range from sandy loams to silt clays.

10. Juniperus scopulorum / Oryzopsis micrantha HT (C):

Juniperus scopulorum is the dominant upperstory vegetation. The undergrowth is dominated by Oryzopsis micrantha and moss. Located on northwest to north facing hillsides having 35-70% slopes and sandy loam to clay loam soils.

11. Populus tremuloides / Betula occidentalis HT (A):

Characterized by Populus tremuloides as the dominant tree species. Frequently above stands of Fraxinus pennsylvanica - Prunus virginiana. Located on upper slopes facing northwest to east on sandy loam to clay loam soils.

12. Hardwood Draws HT (H):

Fraxinus pennsylvanica is the dominant tree species in this HT, with Ulmus americana as the codominant in some stands. Prunus virginiana is the dominant understory tree species. Located in ravines in draws or moderately steep north facing slopes having silt loam to clay loam soils.

13. Brush MU (R):

Small patches of shrubs dominated by Symphoricarpos occidentalis, Prunus virginiana, or Prunus americana. Located on both slopes and grasslands.

14. Rolling Scoria Complex (RS):

Rolling lands influenced by scoria and composed of the following proportion of habitat types:

.25	L HT
.2	WG HT
.2	SC HT
.15	WN HT
.1	J HT
.1	CP HT

Table 2. Continued.

15. Steep Scoria Complex (SS):

Rolling lands influenced by scoria and composed of the following proportion of habitat types:

.3	L HT
.25	J HT
.15	WG HT
.15	SC HT
.1	S HT
.05	CP HT

16. Petrified Forest Complex (PF) - Upland plateaus with numerous petrified stumps and composed of the following habitat types:

.4	WN HT
.3	WG HT
.1	L HT
.05	BB HT
.15	SC HT

17. Introduced Grass MU (IN):

Disturbed areas which have been planted with introduced grasses. The most common grasses occurring at these areas are *Agropyron smithii* and *Bromus inermis*.

18. Prairie Dog Towns MU (PDT):

Areas in or around prairie dog towns where the vegetation has been modified by prairie dogs.

19. Man-Managed MU (MM):

Areas where the vegetation has been modified by human disturbance.

20. *Andropogon gerardii* HT (BB):

Easily recognized by heavy canopy coverage of Andropogon gerardii. Located in moist sites such as depressions and areas of snow accumulation. Soils range from sandy loams to clay loams.

21. *Populus deltoides / Juniperus scopulorum* HT (G):

These are seral communities slowly being replaced by *Fraxinus pennsylvanica*. Located near the Little Missouri River along recent deposits in silt loam soils.

22. River Bottoms MU (RB):

Areas seasonally flooded by the Little Missouri River.

Table 2. Continued.

23. Bare (BARE):

Areas devoid of vegetation for all practical purposes.

24. Shepherdia argentea - (estimated) HT (T-E):

Areas associated with patches of Shepherdia argentea. Total area was estimated from existing habitat types by Norland (1988).

25. Potentilla fruticosa - Schizachirium scoparium - (estimated) HT (PS-E):

Steep upland slopes mostly on northern exposures. Sandy loam soil becoming loamy with depth. Total area was estimated from existing habitat types by Norland (1988).

26. Symphoricarpos occidentalis - (estimated) HT (WB-E):

Same as Brush MU (R). Total area was estimated from existing habitat types by Norland (1988).

27. Schizachirium scoparium - (estimated) HT (S-E):

Same as Schizachirium scoparium HT (L). Total area was estimated from existing habitat types by Norland (1988).

Table 3. Hectarage of Habitat Types/Complexes/Mapping Units within Regions in the South Unit of Theodore Roosevelt National Park. Habitat Types/Complexes/Mapping Units codes are in Table 2.

H.T.	REGION 1	REGION 2	REGION 3	REGION 4	REGION 5	REGION 6
WG	856.10	251.28	447.11	144.44	78.03	199.84
H	50.39	42.29	9.92	19.51	14.49	90.81
L	55.28	40.07	36.54	56.66	42.33	265.93
C	27.32	106.31	38.49	74.10	27.68	8.70
S	28.21	126.55	38.53	69.20	16.75	14.20
WN	31.61	26.18	9.11	3.12	2.55	131.16
R	7.20	0.61	0.00	0.00	0.00	0.81
IN	73.82	81.99	2.91	0.00	0.00	25.98
SC	10.40	32.50	142.86	0.40	16.31	2.51
SS	20.40	225.70	99.52	949.22	768.69	158.40
AA	11.49	96.52	46.99	102.51	20.19	180.42
BS	41.81	47.31	0.00	19.87	0.00	0.00
A	1.62	0.00	0.00	0.00	0.00	0.00
J	26.79	4.94	15.58	43.99	11.21	72.72
RS	0.00	275.12	580.87	174.14	116.11	44.80
MM	0.00	6.88	0.00	0.00	0.00	22.58
PF	0.00	0.00	0.00	0.00	0.00	0.00
G	0.00	0.00	0.00	0.00	0.00	42.41
RB	0.00	0.00	0.00	0.00	0.00	15.01
PDT	41.12	8.70	8.62	1.98	0.00	25.50
BARE	513.24	651.69	641.77	549.58	228.78	273.01
T-E	7.00	3.56	3.44	11.45	5.46	22.95
PS-E	6.11	7.24	14.25	45.77	10.48	2.06
WB-E	42.53	61.47	87.66	88.47	67.87	69.24
BB-E	2.79	4.41	11.61	0.73	7.45	24.73
S-E	95.59	217.24	167.55	173.54	110.16	120.40
TOTAL	1950.82	2318.56	2403.33	2528.68	1544.54	1814.17

Table 3. Continued.

H.T.	REGION 7	REGION 8	REGION 9	REG 1-7	REG 8-9	TOTAL
WG	165.89	316.88	215.30	2142.69	532.18	2674.87
H	22.70	49.62	127.80	250.11	177.42	427.53
L	119.39	379.16	595.80	616.20	974.96	1591.16
C	1.70	41.40	32.50	284.30	73.90	358.20
S	7.28	16.92	79.20	300.72	96.12	396.84
WN	27.92	112.43	418.99	231.65	531.42	763.07
R	0.00	0.00	3.60	8.62	3.60	12.22
IN	0.00	0.00	0.00	184.70	0.00	184.70
SC	3.60	8.30	149.21	208.58	157.51	366.09
SS	0.00	0.00	0.00	2221.93	0.00	2221.93
AA	183.41	247.72	132.42	641.53	380.14	1021.67
BS	0.00	0.00	0.00	108.99	0.00	108.99
A	0.00	0.08	2.31	1.62	2.39	4.01
J	41.44	55.57	105.26	216.67	160.83	377.50
RS	143.55	0.00	0.00	1334.59	0.00	1334.59
MM	5.30	0.00	0.00	34.76	0.00	34.76
PF	0.00	0.00	19.71	0.00	19.71	19.71
G	9.92	27.40	9.11	52.33	36.51	88.84
RB	29.38	30.31	18.70	44.39	49.01	93.40
PDT	69.41	13.40	0.00	155.33	13.40	168.73
BARE	122.79	338.69	478.23	2980.86	816.92	3797.78
T-E	14.81	29.58	43.91	68.67	73.49	142.16
PS-E	3.56	4.41	6.56	89.47	10.97	100.44
WB-E	25.13	73.90	109.80	442.37	183.70	626.07
BB-E	11.57	28.41	42.25	63.29	70.66	133.95
S-E	66.13	146.10	217.00	950.61	363.10	1313.71
TOTAL	1074.88	1920.28	2807.66	13634.98	4727.94	18362.92

2. Vegetative Production (A_i)

Vegetative production (the addition of vegetative tissue in 1 growing season) for major graminoid and shrub species in several HTs/MUs/Complexes in and around TRNP were reported by the Soil Conservation Service (range site guidelines for the North Dakota badlands), Whitman (1979), Hanson et al. (1980), Norland (1984), Marlow et al. (1984), Girard (1985), and Hirsch (1985). These production figures were later collected and revised by Norland (1988).

Most forage species production estimates in individual HTs were taken from Norland (1988) or Marlow et al. (1984). Production for upland and some shrub habitat types in Norland (1988) and Marlow et al. (1984) were based mostly on SCS Range Sites for western North Dakota (USDA SCS 1975). Range Sites provided production estimates for all graminoid species and total forbs but lumped browse species. For selected browse species, Norland (1988) estimated production by the reference unit method. Some important browse species were severely underestimated or underrepresented in these sources. This necessitated obtaining some browse production estimates from a wide variety of published and unpublished literature (Ralston 1960; Nelson 1961;

Hladek 1971; Williams 1976; Murray and Jacobson 1982; Butler 1983; Mastel 1983; Marlow et al. 1984; Girard 1985; Hirsch 1985; Cabral and West 1986; Norland 1988; Sullivan et al. 1988; Irby 1989; Sullivan et al. 1989; Westfall et al. 1989; Creamer 1992; Westfall and Irby 1993). A discussion on how these browse production estimates were used is in the Appendix A.

A few assumptions were used when estimating forage productivity in various HTs. For example, no production estimates were listed for the River Bottoms MU; therefore because of the similarity of habitats, production of the Cottonwood HT (G) was also used for this type. In other cases, we had to subjectively resolve conflicts between published sources. For example, Hardwood Draws HT (H) production was estimated by Sullivan et al. (1988) and Butler (1983). Butler (1983) listed production for only 3 graminoid species on the backslope of hardwood draws: Calamovilfa longifolia, Stipa comata, and Carex spp; Sullivan et al. measured mostly Carex spp., Elymus spp., and Oryzopsis micrantha. Since Carex spp. was also found in hardwood draw transects by Westfall et al. (1989), only production for this species was used. Total graminoid production was retained, however. We felt that this estimate for total graminoid production was reasonable, but values for the other two species could not be reconstructed and were omitted. Total forage production (100%) by habitat type (before it was multiplied by the AUF) is listed in Table 5. as it appears in the forage allocation model. Reliability of production estimates is in Table 6.

3. Allowable Use (U_i)

We decided to allocate forage based on food habits only within the growing season. This is the time when plants were most susceptible to grazing damage (Sampson 1952, Bell 1973). Allowable use was calculated by multiplying estimates of vegetative productivity (growing season edible biomass production) by an Allowable Use Factor (AUF) of 0.35 (35%). By allocating forage at this light/moderate use level during the growing season, ample forage would be left over for fall/winter use. At this time plants are more hardy, can withstand greater utilization, and ungulate consumption declines appreciably. Although utilization at 35% might be considered conservative for some forage species we felt that it was better to err on the side of underuse than overuse, considering the objectives of the forage allocation modeling effort in protecting sensitive plant species.

Sullivan (1988) chose an AUF of 0.35 when estimating the carrying capacity for elk in TRNP during phase 1. Marlow et al. (1984) adopted an AUF of 0.40 when determining the optimum carrying capacity for bison in TRNP. Long-term herbage production was reported to have substantially declined after season-long grazing by cattle at 35-50% utilization levels in the Central Great Plains (Kipple 1964). Payne and Young (1948) observed declines in key browse species in northern Idaho after 6 years of spring/summer clipping of 75% of vegetation and slight declines at the 50% level. They concluded that removal at or below 50% was desirable, especially in spring and summer.

Table 5. Production estimates for forage species in each Habitat Type (HT) as they appear in the forage allocation model. Species acronyms appear in the Appendix E.

PLANT	WG	H	L	RS	SS	AA
AG SPP	757	0	64	311	194	545
BO SPP	252	0	193	236	162	0
BR SPP	0	0	0	0	0	0
CA SPP	84	400	129	108	94	0
EL SPP	0	0	0	0	0	0
KOPY	84	0	64	70	51	0
PO SPP	87	0	0	29	18	34
SCSC	0	0	259	90	140	0
STCO	0	0	194	171	132	0
STVI	84	0	0	31	13	68
OTHER	210	0	193	210	218	35
GRASSTOT	1558	1030	1096	1256	1022	682
FORBSTOT	84	270	64	128	138	112
AR SPP	63	0	13	37	47	246
EULA	11	0	28	12	14	73
PRVI	0	386	0	1	3	0
RHTR	0	56	56	17	24	0
RI SPP	0	26	0	0	2	10
SH SPP	0	12	0	4	3	10
SYOC	5	914	0	17	29	146
OTHER	5	698	32	63	143	20
BROWSTOT	84	2092	129	151	265	505
TOTAL	1726	3392	1289	1535	1425	1299

Table 5. Continued.

PLANT	R	J	BS	A	PDT	IN	S
AG SPP	124	67	196	0	303	841	84
BO SPP	79	27	28	0	101	0	56
BR SPP	0	0	0	0	0	280	0
CA SPP	148	40	34	0	34	0	28
EL SPP	10	0	0	0	0	0	0
KOPY	10	13	22	0	34	0	0
PO SPP	178	0	0	0	35	0	0
SCSC	34	249	0	0	0	0	0
STCO	54	0	28	0	0	0	28
STVI	21	0	39	0	34	0	0
OTHER	241	253	62	0	84	0	89
GRASSTOT	899	649	409	0	625	1121	285
FORBSTOT	44	258	168	0	34	112	112
AR SPP	3	25	244	0	25	63	206
EULA	0	3	73	0	4	11	17
PRVI	82	11	0	99	0	0	0
RHTR	10	28	0	4	0	0	0
RI SPP	11	0	0	6	0	0	21
SH SPP	0	11	0	0	0	0	0
SYOC	856	84	45	25	2	5	45
OTHER	14	459	92	216	2	5	121
BROWSTOT	976	621	454	350	33	84	410
TOTAL	1919	1528	1031	350	692	1317	807

Table 5. Continued.

PLANT	C	WN	BARE	SC	MM	CP	PF
AG SPP	0	555	0	191	0	155	486
BO SPP	0	370	0	286	0	219	286
BR SPP	0	0	0	0	0	0	0
CA SPP	0	92	0	191	0	30	112
EL SPP	0	0	0	0	0	0	0
KOPY	0	93	0	95	0	30	83
PO SPP	0	25	0	22	0	30	45
SCSC	0	0	0	0	0	0	30
STCO	0	185	0	476	0	0	165
STVI	0	92	0	0	0	0	62
OTHER	0	112	0	358	0	60	218
GRASSTOT	0	1524	0	1619	0	524	1487
FORBSTOT	0	185	0	191	0	30	146
AR SPP	0	52	0	35	0	36	46
EULA	1	0	0	0	0	23	6
PRVI	173	0	0	0	0	0	0
RHTR	32	0	0	0	0	0	6
RI SPP	2	0	0	0	0	0	0
SH SPP	18	20	0	0	0	0	8
SYOC	36	21	0	20	0	2	17
OTHER	129	0	0	40	0	1	12
BROWSTOT	391	93	0	95	0	62	95
TOTAL	391	1802	0	1905	0	616	1728

Table 5. Continued.

PLANT	G	RB	BB	T-E	PS-E	WB-E	S-E
AG SPP	0	0	45	12	45	124	84
BO SPP	0	0	0	15	21	79	56
BR SPP	0	0	0	10	34	0	0
CA SPP	0	0	168	27	32	148	28
EL SPP	0	0	0	1	0	10	0
KOPY	0	0	0	5	9	10	0
PO SPP	0	0	112	22	19	178	0
SCSC	0	0	84	424	173	34	0
STCO	0	0	0	6	0	54	28
STVI	0	0	0	5	0	21	0
OTHER	0	0	745	277	127	241	89
GRASSTOT	0	0	1154	804	460	899	285
FORBSTOT	0	0	224	75	189	44	112
AR SPP	0	0	3	17	26	3	206
EULA	0	0	0	2	0	0	17
PRVI	33	33	0	48	40	82	0
RHTR	54	54	0	22	33	10	0
RI SPP	15	15	0	3	2	11	21
SH SPP	9	9	0	231	18	0	0
SYOC	115	115	80	41	200	856	45
OTHER	60	60	29	144	943	14	121
BROWSTOT	286	286	112	508	1262	976	410
TOTAL	286	286	1490	1387	1911	1919	807

Table 6. Status of production estimates of selected forage species used in the Forage Allocation Model within Habitat Types. Status is represented by 1=adequate; 2=sufficient, but should be remeasured; 3=estimated from plant density, production needed; 4=estimated, production needed. Habitat Type codes are in Table 2. Species acronyms appear in the Appendix E.

Forage Spp.	Habitat Type												
	WG	H	L	RS[a]	SS[a]	AA	R	J	BS	A	PDT[a]	IN	S
Graminoids										U			
AG SPP	1		1			1	1	1	1			1	1
BO SPP	1		1				1	1	1	N			1
BR SPP												1	
CA SPP	1	2	1				1	1	1	K			1
EL SPP							1						
KOPY	1		1				1	1	1	N			
PO SPP	1					1	1						
SCSC			1				1	1		O			
STCO			1				1		1				1
STVI	1					1	1		1	W			
Forbs	1	2	1			1	1	1	1	N		1	1
Browse													
AR SPP	3		3			4		3	3			3	3
EULA	1		1			1		4	1			1	1
PRVI		1						1		3			
RHTR		3	1					1		3			
RI SPP		3				3				3			3
SH SPP		3				4		1					
SYOC	4	1				1		1	1	3		4	1

(Continued)

Table 6. Continued.

Forage Spp.	Habitat Type									
	C	WN	BARE[b]	SC	MM[b]	CP	PF[a]	G	RB	BB
Graminoids	U							U	U	
AG SPP		1		1		1				1
BO SPP	N	1		1		1		N	N	
BR SPP										
CA SPP	K	1		1		1		K	K	1
EL SPP										
KOPY	N	1		1		1		N	N	
PO SPP		1		1		1				1
SCSC	O							O	O	1
STCO		1		1						
STVI	W	1						W	W	
Forbs	N	1		1		1		N	N	1
Browse										
AR SPP		3							S	3
EULA	3			3		3			A	
PRVI	3							3	M	
RHTR	3							3	E	
RI SPP	3							3		
SH SPP	3	4						3	A	
SYOC	3	4		4		3		3	S	3
									G	

[a] Production from other HTs or a combination of HTs.
[b] Production nonexistent or not needed.

4. Ungulate Diets (R_j).

Diet selection of ungulates in TRNP was based on microhistological analysis of fecal samples collected by Marlow et al. (1984), Sullivan (1988), and Westfall (1989). Fecal samples of elk, bison, feral horses, mule deer in TRNP were collected during spring (16 Mar-15 Jun), summer (16 Jun-15 Sep), fall (16 Sep-15 Dec) and winter (16 Dec-15 Mar). Each sample was collected from fresh fecal piles throughout the study area. These samples were shipped frozen to the Wildlife Habitat Laboratory in Pullman, Washington for microhistological identification of shrub, forb, and graminoid species composition. A reference collection of graminoids, forbs, and shrubs was collected in by Marlow et al. (1984) for bison food habit analysis, and an additional collection of 104 plant species was made by Sullivan (1988) for aid in identifying elk, mule deer, and feral horse forage items.

The reason for undertaking food habit studies at TRNP was twofold: 1) to evaluate the degree of overlap or partitioning of forage resources; and, 2) to use these data to develop constraints for a forage allocation computer model. Annual production estimates have been made for most graminoid and shrub species within the park; however, forb production has been estimated only to forage class. Because of the variable nature of annual forb production, the difficulty in estimating production, and the relative lack of use by 3 of the 4 ungulate species, we concluded that both the evaluation of forage competition and optimal distribution could be decided on the basis of graminoid and browse species and the forb class. Because food habit studies were conducted when ungulates were at relatively low numbers, it is likely that they had the opportunity to fully express preference for certain dietary items. Dietary preference of ungulates is listed in Table 8.

Spearman's Rank Correlation Coefficients (r_s) were used to compare the similarities of diets between seasons and data sets (Lund 1989). Rank correlations showed that diets from different data sets for the same species were statistically similar. Therefore we combined these food habit studies to derive point estimates (overall means) for diet items.

5. Growing Season Intake (R_j)

Forage intake rates during the growing season were determined for a "typical animal" (based on the mean body size for a population) of each ungulate species from: 1) recorded or reported live weight for 6 age/sex categories; 2) age ratio; 3) sex ratios; 4) a population estimate for mule deer; and, 5) reported daily intake rates.

Bison weights were recorded at 3 roundups in the SU of TRNP in September or October of 1986, 1988, 1990. The weights shown in Table 7. represent mean values for each age/sex category. The estimate of live weight for adult male elk (334 kg) is the average of the mean weight reported by ~~and~~ Murphy (1965); the adult female elk weight (246 kg) is an average of the mean weights reported by Quimby and Johnson (1951), Murphy (1963), and Boyd (1970); yearling male (178 kg) and female (146 kg) weights are from Boyd 1970; and, male calf (123 kg) and female calf (104 kg) are from Murphy (1963).

Feral horse live weights are not well reported in the literature for most age/sex categories. Wolfe et al. (1989) reported mean, live weights for adult females from 4 geographically isolated herds, with the largest size coming from Wyoming. This was used as an approximation of adult female weights in TRNP because of recent and past infusion of domesticated stallions (and the resultant increased body size). From this figure, other age/sex categories were generated from growth curve tables in NAS (1973). Mule deer weights vary considerably over seasons, populations, and geographic areas. Mackie (1964) gave approximate values of hog-dressed mule deer weights from Montana check stations and suggested a correction factor of 1.30 for live weight conversion. These figures were deemed more appropriate for western North Dakota than the limited data from other geographic areas and were used as input in the forage allocation model (Table 7.).

Age and sex ratios for elk were obtained from recent fixed-wing and helicopter surveys by the senior author. Bison age and sex ratios were recorded during 1986, 1988, and 1990 roundups and are recorded in Table 7. Age and sex ratios for feral horse were obtained from a 1991 roundup and are also recorded in Table 7.

Fixed-wing production surveys were flown by North Dakota Game and Fish Dept. on the west side of the Little Missouri River in TRNP during Fall 1962-87, in which all males, females, and fawns were recorded. Later flights utilized different observers and methodology and are not comparable to the earlier flights; so, only the earlier ratios were retained for input into the forage allocation model. Although yearling males were not recorded on these flights, other flights and ground observations indicated a male yearling-adult ratio of about 42.8% (J. Samuelson, N.D. Game and Fish Dept., pers. comm. 1992). A double sampling procedure showed a sampling efficiency of approximately 60% in the badland/upland grassland areas of TRNP (J. Samuelson, N.D. Game and Fish Dept., pers. comm. 1992). These figures were extrapolated to include age/sex ratios and a density estimate for the entire Park. The density of mule deer in the SU of TRNP was estimated to be 824 animals, and this figure was used as the upper and lower bounds for that species in the forage allocation model.

Because forage consumption undergoes seasonal fluctuation in wild, free-ranging animals, peaking in summer and lower in winter, references to late fall/early winter intake rates (% Body Weight (B.W.) daily consumption), where juvenile and yearling animals were about ½ and 1½ years, respectively, were used when possible. Thereby, calculations of ungulate forage consumption for the growing season or for the entire year would be approximately correct and would not have to altered for further model runs.

An attempt was made to find daily intake values for 3 age classes (juvenile; yearling; adult) for each ungulate species. When this was not possible, reported values for certain age classes were given to other age classes. Intake rates presented in Table 7 may represent mean values of more than one study. Reported values for daily intake came from several sources: elk (Geis 1954; Boll 1958); bison (Peters 1958; Richmond et al. 1977; Christopherson et al. 1978; Hawley et al. 1984); feral horses (NAS-NRC 1973; Cymbaluk and Christison 1989; Cymbaluk et al. 1989); mule deer (Alldredge et al. 1974).

Table 7. Ungulate parameters input into the forage allocation model. Estimated weight, herd percentage, and daily intake of each age/sex category of mule deer, bison, feral horses, and elk. These factors (multiplied by 180) were summed to obtain 6-month (180 days) intake of a "typical animal" for each ungulate species. References are given in the text.

Ungulate species	Age/ sex		Weight (kg)	Herd (%)	Daily intake (% B.W.)	Intake - 6 months (kg)
Mule deer	Adult	M	86	16.6	2.1	53.96
	Adult	F	59	30.6	2.1	68.24
	Yearling	M	59	7.1	3.0	22.62
	Yearling	F	53	7.1	3.0	20.32
	Juvenile	M	32	19.3	3.3	36.69
	Juvenile	F	29	19.3	3.3	33.25
	Total					235.08
Bison	Adult	M	563	15.8	1.7	272.20
	Adult	F	472	38.0	1.7	548.84
	Yearling	M	298	11.5	1.7	104.87
	Yearling	F	295	10.0	1.7	90.27
	Juvenile	M	143	13.0	3.1	103.73
	Juvenile	F	127	11.7	3.1	82.91
	Total					1202.82
Feral horse	Adult	M	440	30.3	2.6	623.94
	Adult	F	388	32.1	2.6	582.88
	Yearling	M	290	9.2	2.8	134.47
	Yearling	F	250	9.1	2.8	114.66
	Juvenile	M	190	10.1	2.9	100.17
	Juvenile	F	150	9.2	2.9	72.04
	Total					1628.16
Elk	Adult	M	334	27.0	2.1	340.88
	Adult	F	246	33.0	2.1	306.86
	Yearling	M	178	9.0	2.1	60.56
	Yearling	F	146	9.0	2.1	49.67
	Juvenile	M	123	11.0	2.7	65.76
	Juvenile	F	104	11.0	2.7	55.60
	Total					879.33

Table 8. Estimated forage intake (I) (in parentheses) over the 6 month grazing season (spring and summer) by elk, bison, feral horses, and mule deer, percent diet composition of major forage items, and computed intake of forage items during the growing season (6 mo. I) from these two columns.

	Elk			Bison		
Forage species	Forage I (kg)	% Diet	6 mo. I (kg)	Forage I (kg)	% Diet	6 mo. I (kg)
AGSPP.	(879.33)	8.64	75.97	(1202.82)	19.25	231.54
BOSPP.		1.23	10.82		4.10	49.32
BRSPP.		5.10	44.85		3.15	37.89
CASPP.		5.63	49.51		9.10	109.46
ELSPP.		0.92	8.09		4.50	54.13
KOPY		0.25	2.20		8.55	102.84
POSPP.		2.89	25.41		18.05	217.11
SCSC		2.73	24.01		2.15	25.86
STCO		2.67	23.48		8.25	99.23
STVI		3.00	26.38		3.00	36.08
ARSPP.		0.22	1.93		0.10	1.20
EULA		13.82	121.52		4.05	48.71
PRVI		6.83	60.06		0.00	0.00
RHTR		1.23	10.82		0.00	0.00
RISPP.		2.02	17.76		0.00	0.00
SHSPP.		3.70	32.54		0.10	1.20
SYOC		3.27	28.75		0.00	0.00
TOTAL			564.10			1014.57
GRAMTOT		36.40	320.08		85.25	1025.40
FORBTOT		24.55	215.88		9.25	111.26
BROWTOT		38.75	340.74		5.50	66.16
TOTAL			876.70			1202.82

(Continued)

Table 8. Continued.

Forage species	Horses Forage I (kg)	Horses % Diet	Horses 6 mo. I (kg)	Mule Deer Forage I (kg)	Mule Deer % Diet	Mule Deer 6 mo. I (kg)
AGSPP.	(1628.16)	19.13	311.47	(235.08)	0.75	1.76
BOSPP.		2.44	39.73		0.00	0.00
BRSPP.		3.19	51.94		0.00	0.00
CASPP.		14.45	235.27		0.20	0.47
ELSPP.		0.44	7.16		1.05	2.47
KOPY		3.99	64.96		0.00	0.00
POSPP.		13.92	226.64		3.03	7.12
SCSC		4.57	74.41		0.00	0.00
STCO		17.87	290.95		0.75	1.76
STVI		7.52	122.44		0.47	1.10
ARSPP.		0.00	0.00		12.22	28.73
EULA		4.37	71.15		0.15	0.35
PRVI		0.00	0.00		6.49	15.26
RHTR		0.00	0.00		3.28	7.71
RISPP.		0.00	0.00		3.92	9.22
SHSPP.		0.00	0.00		33.15	77.93
SYOC		0.00	0.00		9.35	21.98
TOTAL			1496.12			175.86
GRAMTOT		93.70	1525.59		7.70	18.10
FORBTOT		1.65	26.86		16.70	39.26
BROWTOT		4.60	74.90		74.60	175.37
TOTAL			1627.35			232.73

[a] Does not equal total forage intake because of the addition of other forage class items (mosses, lichens, seeds, etc.).

Presentation

The data were entered into Quattro Pro as they appear in Table 9. Linear constraint coefficients (forage intake (I) x %diet) for each forage species/category appear as 4 columns under the 4 decision variables (elk, bison, horses, mule deer). The sum of these constraints (multiplied by their objective function coefficient, OBJFUN, each 1 in this case) must be less than or equal to the constant constraint term (LIMITS) (hectarage of HTs x production of each forage species/HT x AUF). Lower and Upper Bounds for each decision variable appears under the objective function coefficients. The solution (total number of ungulates) appears as a single cell. This is divided into 4 decision variable values which appear beside NUMBER UNGULATES and above ELK, BISON, HORSE, and MDEER. Dual Values (DUAL) and Additional Dual Values (ADD DUAL) appear as a column and a row, at the far right and bottom, respectively. These are explained below. Definitions of all input parameters are given in Appendix D.

Table 9. Typical example of the internal structure of the forage allocation model as it appears in a Quattro Pro spreadsheet. Plant species acronyms are given in Appendix E.

PLANT	ELK	BISON	HORSE	MDEER		LIMITS	DUAL
AG SPP	75.97	231.54	311.47	1.76	<=	1582294	0
BO SPP	10.82	49.32	39.73	0	<=	780323.3	0
BR SPP	44.85	37.89	51.94	0	<=	19793.4	1.84E-18
CA SPP	49.51	109.46	235.27	0.47	<=	452463.1	-1.7E-19
EL SPP	8.09	54.13	7.16	2.47	<=	2283.771	0.139665
KOPY	2.2	102.84	64.96	0	<=	231589	0
PO SPP	25.41	217.11	226.64	7.12	<=	179803.9	-2.1E-19
SCSC	24.01	25.86	74.41	0	<=	366970.9	0
STCO	23.48	99.23	290.95	1.76	<=	432299.5	0
STVI	26.38	36.08	122.44	1.1	<=	160981.4	0
GRASSTOT	320.08	1025.4	1525.59	18.1	<=	5165638	7.36E-37
FORBSTOT	215.88	111.26	26.86	39.26	<=	584237.8	0
AR SPP	1.93	1.2	0	28.73	<=	370771.2	0
EULA	121.52	48.71	71.15	0.35	<=	83060.45	0
PRVI	60.06	0	0	15.26	<=	108059	0
RHTR	10.82	0	0	7.71	<=	81862.76	0
RI SPP	17.76	0	0	9.22	<=	25487.18	0
SH SPP	32.54	1.2	0	77.93	<=	31380.1	0
SYOC	28.75	0	0	21.98	<=	488571.3	0
BROWSTOT	340.74	66.16	74.9	175.37	<=	1671278	2.14E-19
TOTAL	876.7	1202.82	1627.35	232.73	<=	7421153	-9.7E-19
						SOLUTION	
OBJFUN	1	1	1	1		858.7054	
LOWBOUND	0	0	0	824			
UPBOUND	10000	10000	10000	824			
NUMBER	0	0	34.70545	824			
UNGULATES	ELK	BISON	HORSE	MDEER			
ADD DUAL	-0.12989	-6.56006	0	0.655028			

Sensitivity Analysis

A sensitivity analysis feature is built into the optimization program within Quattro Pro, allowing the manager to identify what constraints or bounds are most limiting the solution of the objective function and the extent to which they are limiting. "Dual Values" are output after each optimization run and are simply the amount by which the optimal value would be increased (or decreased) if one constant were relaxed (or tightened) one unit. If the Dual Value of a constraint is 0, there is no Dual Value for that constraint - indicating that the constraint is not limiting on the optimal solution. If the Dual Value for the constraint is D (not 0), changing the constant term (plant production available) by 1 will change the optimal value of the objective function by D. (Example: if the Dual Value is +5.0, then adding 1.0 to the limiting plant species production will increase the optimal value by +5.0). Positive Dual Values indicates constraints are limiting; negative Dual Values (also called "surplus") indicates constraints in excess.

The "Additional Dual Value" is the amount by which the optimal value would be increased (or decreased) if a bound (upper or lower) were relaxed (or tightened) one unit. If the Additional Dual Value of a decision variable shows 0, there is no Dual Value for that decision variable - indicating that the constraint is not limiting on the optimal solution. If the Additional Dual Value for the upper or lower bound is D (not 0), changing the active bound (the bound constraining the optimal solution) by 1 will change the optimal value of the objective function by D. Positive values indicate a constraining upper or lower bound. (Example: if the lower bound of an ungulate species is influencing the solution and this bound has an additional dual value of +4.0, then adding 1.0 to the lower bound will raise the optimal solution by 4). Care must be taken in interpreting these results, as the model does not indicate which bound is limiting the solution.

Two types of sensitivity analysis can be assessed through an iterative process. One such analysis can be done by selectively removing the most limiting constraint then rerunning the program. This provides a new set of Dual Values and Additional Dual Values, since the optimization problem has essentially been reformulated. An alternative approach to sensitivity analysis is provided through the iterative addition to the limiting constant constraint (forage species production), decision variable (ungulate species), or bounds (indicated by the Dual Value or Additional Dual Value, respectively). By this method, one can observe how much the constraint or bound is limiting. Davis (1967) had an iterative sensitivity analysis similar to this in a dynamic LP model for deer management.

RESULTS

Model Runs

Optimal solutions were determined with the forage allocation model through a series of runs (no bounds for ungulate species, at preset upper and lower bounds, and by sequentially removing the limiting forage species) (Table 10). Elk numbers in all runs were allowed to range freely because they are more difficult to capture and transplant than bison or feral horses. Lower bounds were used when visitor preference, herd genetics, and species representation were important management considerations; and upper bounds were used when animal damage, or escapement were considerations.

With mule deer numbers set at 824 (reflecting estimated density from aerial surveys) and elk, bison and feral horse numbers allowed to range freely, the model produced a solution (total ungulate numbers) of 859 (1 forage species/category removed) to 7073 (9 forage species/categories) removed (Table 10). In this run only 1 species, Shepherdia, resulted in an infeasible result, and was removed from the model. Forage species were subsequently removed (up to 9) to see how the model would reevaluate the optimal solution. Horse numbers were generally lower than other ungulates (0-488) due to high intake rates (Table 10), especially for forage species with relatively low total production. The forage allocation model selected against horses primarily because of the high intake of Poa spp (226.64 kg), which was one of the last forage species removed from the model, and only selected for horses over bison when total forbs was the limiting species/category. This was because of the relatively low intake of forbs by horses (26.86 kg).

Three runs were make with mule deer numbers set at 824, elk numbers allowed to range freely, bison and horse with lower bounds set at ≥200 and ≥50, ≥200 and ≥100, and ≥300 and ≥100, respectively (Table 10). These runs resulted in solutions (total number of ungulates) of 7060-7073 (9 forage species/categories removed) and in recommended levels of 1939-1949 (3 forage species/categories removed). The recommended level (removing 3 forage species/classes) is due to the poor reported production estimates for Shepherdia and Elymus, and because Bromus is an introduced species. Again, horse numbers were relatively low, usually at the preset lower bounds except when total forbs was the limiting forage species/category. Elk numbers (360-369) were always lower than bison numbers (655-706) at the recommended levels because of the higher intake by elk of the limiting forage species (winterfat, Eurotia lanata). However, after winterfat was removed from the model, elk numbers were always higher than bison numbers primarily because of graminoid species such as Poa spp. and Stipa viridula, which were limiting in later runs and were consumed more heavily by bison than elk.

Three runs were also made with mule deer numbers set at 824, elk numbers allowed to range freely, and bison and horse upper bounds set at ≤300 and ≤100, ≤400 and ≤100, and ≤400 and ≤150, respectively (Table 10). Solutions for these runs were 6892 after the removal of 9 forage species/categories and 1726-1807 at the recommended levels (3 forage classes/categories removed). Unlike earlier runs, the model generally selected for horses (up to the upper bounds) after the first two limiting forage species/categories were removed, except when graminoid species were limiting. This resulted from the difference in preferred species/categories by different ungulates. When browse species (such as Ribes or Prunus virginiana) were limiting, the model set elk numbers (with respect to existing mule deer densities) equal to their production, and allowed bison and horse numbers to reach upper bounds because they did not use these forage species. The model generally produced results with horse numbers at 0 and bison numbers were at or near 0 when graminoid species were limiting because of their high use and because of the relatively low utilization of these by elk.

Optimal Levels

One hundred (100) runs were made with winterfat as the limiting species (Shepherdia, Elymus, Bromus removed). This was the recommended level, due to the insufficient production estimates of Shepherdia and Elymus, and because Bromus was an introduced species. Numbers of bison and horses were changed in increments of 50, with elk numbers allowed to ranging freely. Mule deer numbers were again set at 824, the estimated Park density. This created a 10 x 10 matrix of elk numbers, within the parameters of bison numbers (Y axis) and horse numbers (X axis) (Table 11). At extremely high horse densities infeasible results were obtained die to the higher consumption of winterfat by horses (71.15 kg) compared to that of bison (48.71 kg). Elk numbers ranged from 250-632 depending on bison and horse levels. Equal numbers of horse, bison, and elk (at a mule deer density of 824) was obtained at approximately the 340 level.

Table 10. Forage allocation model runs with upper bounds (≤) and lower bounds (≥) for elk (E), bison (B), feral horses (H), and mule deer (D) set at various levels. Forage species were sequentially removed from the model resulting in different optimal ungulate numbers, limiting forage species (Appendix E), dual value for limiting forage species and additional dual value for the limiting ungulate species. Recommended levels of ungulates are marked with a *.

Forage species removed	Optimal ungulate numbers				Limiting forage species	Dual value	Limiting ungulate species	Additional Dual Value
	E	B	H	D				
				E=free; B=free; H=Free; D=824				
NONE	- Infeasible -							
SH SPP	0	0	35	824	EL SPP	0.140	D	0.655
EL SPP	0	522	0	824	BR SPP	0.026	D	1.000
BR SPP*	378	757	0	824	EULA	0.008	D	0.977
EULA	1007	683	0	824	RI SPP	0.050	D	0.509
RI SPP	1590	615	0	824	PRVI	0.015	D	0.743
PRVI	2496	0	488	824	FORBSTOT	0.004	D	0.808
FORBSTOT	4426	283	0	824	PO SPP	0.004	D	0.508
PO SPP	4218	1353	0	824	STVI	0.026	D	0.810
STVI	4052	2110	87	824	KOPY	0.006	D	0.535
				E=free; B≥200; H≥50; D=824				
NONE	- Infeasible -							
SHEP SP	- Infeasible -							
EL SPP	0	454	50	824	BR SPP	0.026	D	1.000
BR SPP*	369	706	50	824	EULA	0.008	D	0.977
EULA	1007	631	50	824	RI SPP	0.050	D	0.509
RI SPP	1590	563	50	824	PRVI	0.015	D	0.743
PRVI	2415	200	305	824	FORBSTOT	0.004	D	0.808
FORBSTOT	4425	231	50	824	PO SPP	0.004	D	0.508
PO SPP	4244	1164	50	824	STVI	0.026	D	0.810
STVI	4052	2110	87	824	KOPY	0.006	D	0.535
				E=free; B≥200; H≥100; D=824				
NONE	- Infeasible -							
SH SPP	- Infeasible -							
EL SPP	0	385	100	824	BR SPP	0.026	D	1.000
BR SPP*	360	655	100	824	EULA	0.008	D	0.977
EULA	1007	579	100	824	RI SPP	0.050	D	0.509
RI SPP	1590	511	100	824	PRVI	0.015	D	0.743
PRVI	2415	200	305	824	FORBSTOT	0.004	D	0.808
FORBSTOT	4244	200	100	824	PO SPP	0.039	D	0.720
PO SPP	4269	976	100	824	STVI	0.026	D	0.810
STVI	4055	2081	100	824	CA SPP	0.008	D	0.687

Table 10. Continued.

Forage species removed	Optimal ungulate numbers E	B	H	D	Limiting forage species	Dual value	Limiting ungulate species	Additional Dual Value
E=free; B≥300; H≥100; D=824								
NONE	- Infeasible -							
SH SPP	- Infeasible -							
EL SPP	0	385	100	824	BR SPP	0.026	D	1.000
BR SPP*	360	655	100	824	EULA	0.008	D	0.977
EULA	1007	579	100	824	RI SPP	0.050	D	0.509
RI SPP	1590	511	100	824	PRVI	0.015	D	0.743
PRVI	2375	300	214	824	FORBSTOT	0.004	D	0.808
FORBSTOT	3390	300	100	824	PO SPP	0.039	D	0.720
PO SPP	4269	975	100	824	STVI	0.026	D	0.810
STVI	4055	2081	100	824	CA SPP	0.008	D	0.687
E=free; B≤300; H≤100; D=824								
NONE	- Infeasible -							
SH SPP	0	0	35	824	EL SPP	0.140	D	0.655
EL SPP	188	300	0	824	BR SPP	0.022	D	1.000
BR SPP*	502	300	100	824	EULA	0.008	D	0.997
EULA	1007	300	100	824	RI SPP	0.056	D	0.481
RI SPP	1590	300	100	824	PRVI	0.017	D	0.746
PRVI	2389	300	100	824	FORBSTOT	0.005	H	0.876
FORBSTOT	4426	283	0	824	PO SPP	0.004	D	0.508
PO SPP	4401	300	100	824	BROWSTOT	0.003	B	0.806
BROWSTOT	6068	0	0	824	STVI	0.038	D	0.958
E=free; B≤400; H≤100; D=824								
NONE	- Infeasible -							
SH SPP	0	0	35	824	EL SPP	0.140	D	0.655
EL SPP	103	400	0	824	BR SPP	0.022	D	1.000
BR SPP*	462	400	100	824	EULA	0.008	D	0.997
EULA	1007	400	100	824	RI SPP	0.056	D	0.481
RI SPP	1590	400	100	824	PRVI	0.017	D	0.746
PRVI	2338	400	100	824	FORBSTOT	0.005	H	0.876
FORBSTOT	4426	283	0	824	PO SPP	0.004	D	0.508
PO SPP	4381	400	100	824	BROWSTOT	0.003	B	0.806
BROWSTOT	6068	0	0	824	STVI	0.038	D	0.958

Table 10. Continued.

Forage species removed	Optimal ungulate numbers				Limiting forage species	Dual value	Limiting ungulate species	Additional Dual Value
	E	B	H	D				
	E=free; B≤400; H≤150; D=824							
NONE	- Infeasible -							
SH SPP	0	0	35	824	EL SPP	0.140	D	0.655
EL SPP	103	400	0	824	BR SPP	0.022	D	1.000
BR SPP*	433	400	150	824	EULA	0.008	D	0.997
EULA	1007	400	150	824	RI SPP	0.056	D	0.481
RI SPP	1590	400	150	824	PRVI	0.017	D	0.746
PRVI	2347	370	150	824	FORBSTOT	0.004	D	0.812
FORBSTOT	4426	283	0	824	PO SPP	0.004	D	0.508
PO SPP	4370	400	150	824	BROWSTOT	0.003	B	0.806
BROWSTOT	6068	0	0	824	STVI	0.038	D	0.958

Table 11. Matrix of feasible elk numbers for a forage allocation optimization problem based on winterfat utilization and availability with bison and horses set at various levels and an implied mule deer density of 824. Gaps in the matrix indicate infeasible solutions.

Bison numbers	Horse numbers									
	50	100	150	200	250	300	350	400	450	500
50	632	603	573	544	515	485	456	427	398	368
100	612	583	553	524	495	465	436	407	378	348
150	592	562	533	504	475	445	416	387	358	328
200	572	542	513	484	455	425	396	367	338	308
250	552	522	493	464	435	405	376	347	318	250
300	532	502	473	444	415	385	356	327	268	
350	512	482	453	424	395	365	336	287		
400	492	462	433	404	374	345	306			
450	472	442	413	384	354	325				
500	452	422	393	364	334					

Variation in Objective Function Coefficients

All previous model runs were made with coefficients of ungulate species in the objective function equal to 1 (i.e. all ungulate species were weighted equally). To observe the effects of changes in objective function coefficients, ungulates were weighted in terms of overall intake, daily intake, winterfat intake, biomass, and a hypothetical visitor preference rating (Table 12). Coefficients >1.00 weighted for, and coefficients <1.00 weighted against, ungulate species.

Overall intake, daily intake, winterfat intake, and biomass all resulted in runs with 0 values for horses. This was due to the high consumption rates of horses compared to bison. Biomass weighted horses (0.15) slightly more than bison (0.14), but was not enough to affect the outcome. These runs gave similar results to allowing bison, elk, and horses numbers to range freely with objective function coefficients of 1. Only runs with the objective function weighted in terms of a hypothetical visitor preference (weighted heavily for horses) resulted in 0 value for bison, and a value of 740 for horses. In all runs, the model produced solutions with elk >0 (either at 248 or 378) because of the higher consumption of some forage species (PO SPP, STVI, FORBSTOT) by horses and/or bison which limited their numbers.

Table 12. Objective function coefficients based on intake, biomass, and visitor preference and results of forage allocation model runs for elk (E), bison (B), feral horses (H) and mule deer (D) at the winterfat level.

	Objective Function				Ungulate Numbers			
	E	B	H	M	E	B	H	M
Overall Intake	0.27	0.19	0.14	1.00	378	757	0	824
Daily Intake	0.91	1.00	0.74	0.74	378	757	0	824
Winterfat Intake	0.40	1.00	0.68	1.00[a]	378	757	0	824
Biomass	0.23	0.14	0.15	1.00	378	757	0	824
Visitor Preference	2.00	3.00	4.00	1.00	248	0	740	824

[a] Coefficient arbitrarily set at 1.00.

Sensitivity Analysis

A sensitivity analysis was built into Quattro Pro in terms of Dual Values (sensitivity for forage species) and Additional Dual Values (sensitivity for ungulate species). Although Dual Values for most forage species varied from run to run, the value for the limiting forage species at the recommended level (Eurotia lanata, 0.008) remained constant for each run (Table 10). A change in winterfat production of 1 kg would have resulted in a change in the total solution (number of ungulate species) of only 0.008 animals; and, a change of 10,000 kg would have resulted in a change of 80 additional animals. However, the next limiting forage species, Poa, also influenced the solution.

To deduce which forage species would become next limiting, a sensitivity analysis was developed by the iterative addition of an increasing amount of winterfat production (Table 13). This allows managers to identify the change in production estimates that would affect the model outcome. In this instance, winterfat is used. With up to 70,000 extra kg of winterfat production added the first, second, and third limiting forage species remained Eurotia lanata, Poa spp, and total browse. The Dual Values for these species did not change. Only when 80,000 kg of additional forage was added did Eurotia lanata cease to become limiting, with Ribes spp, Poa spp and Total forbs as the limiting species. After the removal (or addition of enough production to make it non-limiting), Ribes spp replaced winterfat as the limiting forage species.

A sensitivity analysis was also developed to evaluate the bounds of ungulate species. Mule deer was generally the limiting ungulate species to higher solutions (ungulate species) because of the upper (but not the lower) bounds of 824 placed on them. If the upper bound of mule deer was raised by 1 the solution would have changed by the Additional Value. This value was 1.000 when mule deer did not eat any of the limiting forage species. At the recommended level, the additional dual value for mule deer was 0.997, indicating that if the upper bounds of mule deer was raised by 100, the total solution was have increased by 99.7 (Table 10).

To observe when the mule deer upper bounds ceased to be limiting, a sensitivity analysis was developed by the iterative increase in the their upper bounds (Table 14). With an addition of up to 1100 animals, mule deer still limited the solution and retained an additional value of 0.977. However, with an addition of 1200 mule deer, the additional value for this species fell to 0.508, and the solution did not increase as much. With the addition of 2,000, mule deer were no longer limiting the solution.

Table 13. Sensitivity analysis of the changes in the optimal solution and limiting forage species with iterative addition of winterfat production. Species acronyms are in Appendix E.

Winterfat production	1st limiting spp		2st limiting spp		3st limiting spp		Solution
	Spp	Dual Value	Spp	Dual Value	Spp	Dual Value	
83060	EULA	0.008	PO SPP	0.003	BROWSE	1.61 E-20	1958
93060	EULA	0.008	PO SPP	0.003	BROWSE	1.61 E-20	2035
103060	EULA	0.008	PO SPP	0.003	BROWSE	1.61 E-20	2111
113060	EULA	0.008	PO SPP	0.003	BROWSE	1.61 E-20	2187
123060	EULA	0.008	PO SPP	0.003	BROWSE	1.61 E-20	2267
133060	EULA	0.008	PO SPP	0.003	BROWSE	1.61 E-20	2340
143060	EULA	0.008	PO SPP	0.003	BROWSE	1.61 E-20	2416
153060	EULA	0.008	PO SPP	0.003	BROWSE	1.61 E-20	2492
163060	RI SPP	0.050	PO SPP	0.005	FORBS	2.76 E-19	2515

Table 14. Sensitivity analysis of the changes in the optimal solution and limiting ungulate species with iterative addition of mule deer (MDEER) upper bounds. Species acronyms are in Appendix E.

MDEER Added	MDEER Upper Bounds	MDEER Number	Limiting Ungulate		Solution
			Spp	Addition Dual Value	
0	824	824	MDEER	0.977	1959
400	1224	1224	MDEER	0.977	2349
800	1624	1624	MDEER	0.977	2740
1100	1924	1924	MDEER	0.977	3033
1200	2024	2024	MDEER	0.508	3125
1600	2424	2424	MDEER	0.508	3329
2000	2824	2724	NONE	--	3481

Discussion

The forage allocation model provided several ways of distributing allowable forage productivity to ungulate species: 1) allowing ungulate numbers to range freely, 2) setting lower bounds, 3) setting upper bounds, 4) fixed values used iteratively, 5) altering objective function coefficients, and 6) any combination of these. The model provides an array of feasible solutions, however, the optimal solution could only be determined by management goals.

Although we identified Shepherdia and Elymus as the 2 most limiting forage species (with Bromus third), the most useful method of allocating forage appeared to be based on using winterfat, the fourth most limiting species. Forage values were insufficient or inadequate for Shepherdia spp. and Elymus spp., and Bromus spp. could be discarded because it is an introduced species. Shepherdia is the most important browse species to mule deer, and Elymus was one of the few graminoid species extensively used by all ungulate species. Both Shepherdia and Elymus should be monitored by managers and production values should be obtained in appropriate habitat types.

The determination of optimal ungulate levels based on the sequential removal of limiting forage species/categories beyond limits imposed by winterfat were useful academic exercises and important in showing how the model functioned, but they have limited management implication. For Theodore Roosevelt National Park has been mandated to preserve native plant communities and species. Winterfat has been identified as a decreaser under intensive grazing (Appendix B) and ungulate numbers that are tolerated by winterfat should be tolerated by most plant species. Some species/categories that became limiting after winterfat should also be monitored. Total vegetational categories (GRASSTOT, FORBSTOT, BROWSTOT) provide upper estimates for vegetational utilization. Ungulate numbers should not be allowed to build beyond these levels.

Model runs where ungulate numbers were allowed to range freely generally provided results we expected. Horse numbers were low in most runs due to high overall intake. Elk numbers were higher than bison or horses due to lower intake by elk. However, due to competition of elk with mule deer for some browse species, and elk with bison for some later-limiting graminoid species, the model selected for at least a representative number of bison instead of allocating all forage to elk. It can be concluded from this and other runs that horses are energetically inefficient, and to optimize total ungulate numbers, they must be below bison and elk population levels.

Model runs with set lower bounds will probably be more useful to managers than free runs - because allowing for minimum ungulate numbers more closely approximate Park goals for maintaining genetic diversity, visitor visibility, and species representation. With lower bounds set, the model in this case performed somewhat like the earlier example, allocating most forage to elk and bison. However, by raising the lower limit of bison and horses, the total solution did not decrease at the same rate - indicating that some ungulates were not as limited by the current "limiting forage species/category." This iterative process could be used to seek a higher number of ungulates.

When runs were constrained by upper bounds on bison and horses, the solution decreased. This was due to the restrictions placed on the model to allocate forage optimally. This approach, however, may have some validity since Park goals are to maintain ungulates at manageable levels, and to minimize damage to Park resources (other than forage), visitor conflicts, and escapement. The best approach to assure that all considerations are taken into account is to have upper and lower bounds for each ungulate species

The other major approach to forage allocation used was to set population levels for bison and horses (with mule deer density at 824) and allow elk numbers to range freely. This approach has some utility because bison and horses have been in the Park longer and problems have already been encountered and dealt with at both higher and lower numbers. But elk are relatively new to the Park and the optimal stocking level has yet to be determined. Allowing the model to select elk numbers after setting appropriate horse and bison numbers could be a effective management tool. The matrix created by this procedure was relatively homogeneous (i.e. an increase in 1 ungulate species by a set amount corresponding increase in elk numbers at a set amount). However, an increase in horses by a set amount was not equivalent to an increase in bison by the same amount. Once again, higher horse numbers resulted in lower total solutions.

Changes in objective function coefficients had limited utility by themselves. When coefficients were altered from 1, in runs using winterfat as the constraining forage category, the model did not allocated forage to horses. This is contrary to Park management goals and is unacceptable. The only way to include horses in the solution was to weight visitor preference for horses much higher than other ungulate species. Manipulations of objective function coefficients could potentially be used if upper and lower bounds were set for each ungulate species. These areas need to be explored further.

The sensitivity analysis provided with the Dual Values and Additional Dual Values in the forage allocation model provided ways to evaluate flexibility in constants or decision variables. Addition information on vegetative productivity could be evaluated prior to inclusion in the model; by determining the amount needed to significantly alter the solution. Also, by selectively removing forage species/categories, changes in ungulate numbers can also be observed. Therefore, Dual Values in combination with an iterative removal of forage species/categories could provide very useful information on the sensitivity of the model. Additional Dual Values also were important by showing the limiting ungulate species. However, in most instances this was mule deer, at an absolute density of 824, which gave little flexibility for altering this parameter.

In conclusion, the forage allocation model provides resource managers with an automated, systematic way to work with basic wildlife-vegetational relationships and a tool for making management decisions. The model has some obvious limitations of which the manager should be aware. These include: 1) the restriction of the model to linear functions, 2) lack of stochasticity in constraints and reliance wholly on deterministic inputs, 3) the inability of the model to account for intra-specific and inter-specific affects on grazing behavior.

However, the benefits of using a linear programming model are many and outweigh the disadvantages. The model allows managers: 1) the ability to assemble and inventory, in a systematic way, all data on ungulate-vegetation interactions in an area, 2) to rapidly assess data voids in ungulate-vegetational systems, 3) to explore complex ecological relationships 4) to quickly obtain feasible solutions for the mix of ungulates in an attempt to derive an optimal solution, 5) to justify management-related decisions based on available data, 6) to incorporate new information as it is collected.

Management Recommendations

In order to make best use of this forage allocation model, Park resource managers should consider the following recommendations:

1. Consider output from the forage allocation model a "first approximation" of optimal stocking levels. The model should be considered a flexible management tool to be refined as new data are gathered.

2. Monitor existing vegetation transects at TRNP according to a fixed schedule to evaluate trends in coverage and frequency of forages that were determined to be important in the model. The most important forage categories to consider in monitoring are:

Shepherdia spp. - upland transects.
Elymus spp. - hardwood transects, cottonwood transects.
Eurotia lanata - upland transects, shrub transects.
Ribes spp. - hardwood transects, cottonwood transects.
Prunus virginiana - hardwood transects, juniper transects, cottonwood transects.
Poa spp. (natives) - upland transects.
Stipa viridula - upland transects, cottonwood transects.

Any significant decline in these species over a period of years should alert managers to possible overstocking problems.

3. Model parameters and ungulate populations should be continually reevaluated. Production estimates in TRNP should be obtained for important forage species in all habitat types. Species of first priority are marked with a 3 or 4, or are listed as "unknown," in Table 6.

4. Census efforts for ungulates should be maintained with emphasis on changes in distribution and population structure that could signal population problems.

5. Non-biological factors should be tested for incorporation in the model. For example, costs of managing excess animals, risks to visitors and visitor preference could be input by manipulating objective function coefficients.

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Appendix A

Browse Production Estimates

All browse species (or species groups) which contributed ≥3% of the spring/summer diet of any ungulate species were broken into respective stratums (herbaceous layer, shrub layer, and sapling layer) in which they occurred (Table 15). Absolute density (number/hectare) of stems of various shrub species were obtained for forested HTs (Ralston 1960, Nelson 1961, Girard 1985, Sullivan et al. 1988, and Westfall et al. 1989) and upland/shrub HTs (Hirsh 1985). Presence of some shrub species in upland/shrub HTs was indicated by SCS Range Sites (USDA SCS 1975). Density estimates were placed in the respective stratum according to the literature source (Table 15).

Vegetation was broken into 3 layers: herbaceous (<1 m), shrub (1-2 m), and sapling (>2m, <10cm dbh) (Sullivan 1988, Sullivan et al. 1988b, Westfall et al. 1989). This division differed from Girard (1985) in the shrub stratum (>30 cm, <2 m) and with Hirsch (1985) in the herbaceous stratum (≤20 cm). Only a few species were from Nelson (1961) (who combined the shrub/sapling stratum) and Ralston (1960) (who did not give dimensions for stratums). Because of this discrepancy in stratum categories, species density estimates in question were placed a lower category, to allow for a conservative estimate of browse production.

Browse species density estimates were then multiplied by estimates of individual plant production (per stem) (Table 15). These estimates were obtained from a review of the literature (Table 15) and from clipping by the authors (Table 15). The authors clipped selective shrubs on the Northern Range outside of Yellowstone National Park, near Gardiner, MT, in height classes thought to represent shrubs observed at TRNP. These samples were oven-dryed for 48 hrs at 60 C, and weighed to nearest 0.1 g.

For upland HTs, only total browse production identified in Norland 1988, Marlow et al. 1984, or the Range Sites were used. Newly generated production estimates were then given to browse species if they fit within the total browse production identified by these sources. If the estimate was too high, it was lowered to fit within this parameter. Estimates of shrub production (generally <5 kg/ha) was also made for some shrub species that were identified as being present within the HT but no production estimate was available.

Table 15. Reported selective browse species productivity (Marlow et al. 1984, Norland 1988), reported density (No./ha), and derived (in parentheses) and estimated (in brackets) productivity for habitat types. Density estimates were from Ralston 1960, Nelson 1961, Girard 1985, Hirsch 1985, Sullivan et al. 1988, Westfall et al. 1989. Plant production citations are footnoted. Habitat Type codes are in Table 2, and plant species acronyms are in Appendix E.

		Habitat Type							
		WG		H		L		AA	
Sp.	Production (g/plant)	No./ha	kg/ha	No./ha	kg/ha	No./ha	kg/ha	No./ha	kg/ha
Amal					94				
h	4.5[a]			10595					
sh	30.7[a]			2619					
sa	30.7[a]			931					
Arca									224
h	6.0[b]	2667	[25]					48200	
sh	35.7[b]	225	[15]					2765	
Ardr									[2]a
h	2.2[c]								
Arfr		+				+			[10]a
h	0.4[c]	28333	[23]			2500	[8]		
Arlu									
h						2000	[5]		
Artr									[10]a
h	6.0[b]								
sh	35.7[b]								
At spp									
sh									
Chna						+	[2]		
h	57.0[c]								
sh	57.0[c]								
Clli									
sh									
Eula		+	11				28		73
h	5.4[d]	1000							
Frpe					559				
h	6.6[e]			10833					
sh	41.6[e]			1190					
sa	73.3[e]			1611					
Gusa						+	[2]		[10]a
sh	4.0[f]								
Juco									
h				238	[5]				
Juho						+	[2]		
sh									
Jusc						+	[2]		
sh				119	[5]				
Prvi					386				
h	4.2[c]			133214					
sh	45.3[c]			11429					
sa	42.9[c]			3639					

Table 15. Continued.

		Habitat Type							
		WG		H		L		AA	
Sp.	Production (kg/plant)	No./ha	kg/ha	No./ha	kg/ha	No./ha	kg/ha	No./ha	kg/ha
Rhtr						+	56		
h	15.0[c]			3095	(46)				
sh	15.0[c]			595	(9)				
sa	15.0[c]			83	(1)				
Ri spp									
h	4.2[c]			4643	(20)			600	[10]
sh	4.2[c]			1190	(5)				
sa	4.2[c]			97	(1)				
Ro spp		+	[5]		35				
h	11.8[c]			2262		2000	(24)		[10]a
sh	11.8[c]								
Sh spp				282	(12)				[10]a
h	44.1[h]								
sh	44.1[h]								
Sy spp		+	[5]		914				146
h	1.0[i]			83810				23200	
sh	1.0[i]							121	
Tora									
h									
Yugl									
sh									
Total			84		2092		129		505

Table 15. Continued.

Sp.	Production (kg/plant)	Habitat Type: J No./ha	J kg/ha	BS No./ha	BS kg/ha	A No./ha	A kg/ha	S No./ha	S kg/ha
Amal									
h	4.5	472	(2)			11111	(50)		
sh	30.7								
sa	30.7					504	(15)		
Arca			11		28				45
h	6.0			5600				1000	
sh	35.7			135					
Ardr									
h	2.2	21500	[7]	3000	[5]			667	[3]
Arfr		+		+				+	
h	0.4	11500	(5)	122200	[15]			52000	[18]
Arlu									
h		1250	[2]						
Artr				+	196			+	140
h	6.0			143400				3333	
sh	35.7			823				404	
At spp				+	84			+	73
h				1800				77333	
sh								1439	
Chna				+				+	45
h	57.0			600	[5]			13000	
sh	57.0							337	
Clli									
sh									
Eula		+	[3]		73				17
h	5.4			3000					
Frpe									
h	6.6					4879	(32)		
sh	41.6								
sa	73.3					557	(41)		
Gusa		+	[3]	+	[3]			+	[3]
sh	4.0								
Juco									
h		17	[1]						
Juho		+	448						
sh									
Jusc									
sh						298	[3]		
Prvi			11						
h	4.2					21928	(92)		
sh	45.3	34							
sa	42.9					157	(7)		

Table 15. Continued.

Sp.	Production (kg/plant)	J No./ha	J kg/ha	BS No./ha	BS kg/ha	A No./ha	A kg/ha	S No./ha	S kg/ha
Rhtr		+	28						
h	15.0					294	(4)		
sh	15.0								
sa	15.0	202							
Ri spp									
h	4.2							5000	(21)
sh	4.2					1411	(6)		
sa	4.2								
Ro spp									
h	11.8					6349	(75)		
sh	11.8	101	(1)						
Sh spp			11						
h	44.1								
sh	44.1	17							
Sy spp			84		45				45
h	1.0			600		24633	(25)	4333	
sh	1.0	438		13					
Tora									
h		4500	[4]						
Yugl									
sh									
Total			621		454		350b		410

Table 15. Continued.

		Habitat Type							
		C		WN		SC		CP	
Sp.	Production (kg/plant)	No./ha	kg/ha	No./ha	kg/ha	No./ha	kg/ha	No./ha	kg/ha
Amal		238	(1)						
h	4.5								
sh	30.7								
sa	30.7								
Arca				+	[15]				
h	6.0							3000	(18)
sh	35.7								
Ardr									
h	2.2			11200	[10]	24333	[10]	3750	[3]
Arfr				+		+		+	
h	0.4			66400	(27)	33667	[10]	29250	[8]
Arlu									
h						102667	[15]	750	[1]
Artr								+	
h	6.0							1000	(6)
sh	35.7								
At spp									
h									
sh									
Chna		476	(27)						
h	57.0								
sh	57.0								
Clli									
sh									
Eula		250	(1)					+	
h	5.4							4250	(23)
Frpe									
h	6.6	1429	(9)						
sh	41.6								
sa	73.3	472	(35)						
Gusa								+	[1]
sh	4.0								
Juco									
h		15714	[20]						
Juho									
sh		103	[3]						
Jusc									
sh		2857	[10]						
Prvi		2361	[10]						
h	4.2								
sh	45.3	27143	(114)						
sa	42.9	1190	(54)						
sa		111	(5)						

Table 15. Continued.

		Habitat Type							
		C		WN		SC		CP	
Sp.	Production (kg/plant)	No./ha	kg/ha	No./ha	kg/ha	No./ha	kg/ha	No./ha	kg/ha
Rhtr									
h	15.0	2143	(32)						
sh	15.0								
sa	15.0								
Ri spp									
h	4.2	476	(2)						
sh	4.2								
sa	4.2								
Ro spp						+			
h	11.8	1190	(14)			21667	[40]		
sh	11.8								
Sh spp		412	(18)	+	[20]				
h	44.1								
sh	44.1								
Sy spp				+	[21]	+	[20]		
h	1.0	36190	(36)					2000	(2)
sh	1.0								
Tora									
h									
Yugl									
sh									
Total			391		93		95		62

Table 15. Continued.

		Habitat Type			
		G		BB	
Sp.	Production (kg/plant)	No./ha	kg/ha	No./ha	kg/ha
Amal					
h	4.5	514	(2)		
sh	30.7				
sa	30.7				
Arca					
h	6.0				
sh	35.7				
Ardr					
h	2.2				
Arfr					
h	0.4				
Arlu					
h				13250	[3]
Artr					
h	6.0				
sh	35.7				
At spp					
h					
sh					
Chna					
h	57.0				
sh	57.0				
Clli					
sh					
Eula					
h	5.4				
Frpe					
h	6.6	2857	(19)		
sh	41.6				
sa	73.3	28	(2)		
Gusa					
sh	4.0				
Juco					
h					
Juho					
sh		210			
Jusc					
sh		2143	[5]		
Prvi		238	[5]		
h	4.2	1278	[5]		
sh	45.3				
sa	42.9	7619	(32)		
sh					
sa		19	(1)		

Table 15. Continued.

		Habitat Type			
		G		BB	
Sp.	Production (kg/plant)	No./ha	kg/ha	No./ha	kg/ha
Rhtr					
h	15.0	2143	(32)		
sh	15.0	1429	(21)		
sa	15.0	28	(1)		
Ri spp					
h	4.2	3571	(15)		
sh	4.2				
sa	4.2				
Ro spp					
h	11.8	1905	(22)	21000	[28]
sh	11.8				
Sh spp					
h	44.1	210	(9)		
sh	44.1				
Sy spp					
h	1.0	114762	(115)	73500	(74)
sh	1.0			5700	(6)
Tora					
h				2000	[1]
Yugl					
sh					
Total			286		112

[a] Williams 1976; [b] Creamer 1992; [c] Westfall and Irby 1993; [d] Cabral and West 1986; [e] Sullivan et al. 1989; [f] Murray and Jacobson 1982; [g] Irby 1989; [h] Hladek 1971; [i] Mastel 1983.

Appendix B

Table 16. Origin (N=Native, I=Introduced), Type of Plant (C=Cool Season, W=Warm Season, S=Sedge) and Grazing Response (INC=increaser, INV=Invader, DEC=Decreaser) for most major forage species in the forage allocation model. Adapted from Yaeger et al. (1976).

Forage species	Origin	Type of Plant	Grazing Response
Graminoids			
Agropyron sp. (AG SPP)			
A. smithii (most)	N	C	INC
A. cristatum	I	C	INV
A. subsecundum	N	C	DEC
Bouteloua sp. (BO SPP)			
B. gracilis (most)	N	W	INC
B. curtipendula	N	W	DEC
Bromus sp. (BR SPP)			
B. inermis	I	C	INV
B. japonicus	I	C	INV
B. tectorum	I	C	INV
Carex sp. (CA SPP)			
C. filifolia (most)	N	S	INC
C. eleocharis	N	S	INC
C. heliophila			
Elymus sp. (El SPP)			
E. canadensis	N	C	DEC
E. virginicus (most)			
Koeleria pyramidata	N	C	INC
Poa sp. (PO SPP)			
P. pratensis	I	C	INV
P. arida			
Schizachyrium scoparium	N	W	DEC
Stipa comata	N	C	INC
Stipa viridula	N	C	DEC
Browse			
Artemisia sp. (AR SPP)			
A. cana	N	W	DEC
A. dracunculus			
A. frigida	N	W	INC
A. ludoviana			
A. tridentata (most)	N	W	INC
Eurotia lanata	N	W	DEC
Prunus virginiana	N	C	INC
Rhus trilobata	N	C	INC

(continued)

Table 16. Continued.

Forage species	Origin	Type of Plant	Grazing Response
Browse (cont.)			
Ribes sp. (RI SPP)			
R. odoratum	N		
R. setosum (most)	N		
Sheperdia sp. (SH SPP)			
S. argentea (most)	N		
S. canadensis	N		
Symphoricarpos sp. (SY SPP)			
S. occidentalis (most)	N	W	INC
S. albus	N	W	INC

Appendix C

Quattro Pro Commands

Procedure (steps)	Description of command
Initiation:	
step 1. cd\qpro	(DOS command - changes to preferred directory)
step 2. q	(keyword - invokes Quattro Pro)
step 3. /F D	(/(F)ile (D)irectory - changes file directory)
step 4. a:	(new directory = a:, allows storage of data on disk)
step 5. /F R	(/(F)ile (R)etrieve - retrieves file in a: directory)
Save and Resume:	
step 1. /F S	(/(F)ile (S)ave - saves file)
step 2. R	((R)eplace - replaces a file with same name. Warning! if backup copies are desired use File Save As command and change name)
Save As:	
step 1. /F A	(/(F)ile Save (A)s- saves file)
step 2. (directrory:\ <file name>)	(Saves file as the specified directory and filename.
Functions:	
Summation:	
@SUM(A1..C7)	(Sums the block A1 (upper left corner) to C7 (lower right corner) and places the value in the cell where the cursor is located. Warning! this procedure will overwrite previous cell contents.)
Averaging:	
@SUM(A1..C7)/3	(Will sum and then average the block A1 (upper left corner) to C7 (lower right corner)3 columns, placing the value in the cell where the cursor is located). Warning! this procedure will overwrite previous cell contents.)
Advanced Math Techniques:	
Multiply a Matrix:	
step 1. /T A M	(/(T)ools (A)dvanced Math (M)ultiply)
step 2. <esc>	(escape - clears a field if frozen)
step 3. <arrow>	(move cursor to beginning of 1st matrix field, upper left corner).
step 4. <.>	(type a . - indicating beginning of block).
step 5. <arrow>	(shade entire block).
step 6. <arrow>	(move to beginning of 2nd matrix, upper left corner).
step 7. <.>	(type a ., and also shade entire block).
step 8. <arrow>	(move to upper left corner of destination block. Warning! destination block should be empty).

Quattro Pro Commands (Continued)

Procedure (steps)	Description of command
Moving Cursor:	
1. <Tab>	(Tabs to right 1 page, same row).
2. <Shft Tab>	(Tabs to left 1 page, same row).
3. <Home>	(Moves to 1st cell of the spreadsheet. Warning! use inner keypad).
4. <Page Down>	(Moves down 1 page. Warning! use inner keypad).
5. <Page Up>	(Moves up 1 page. Warning! use inner keypad).
Positioning Cell Values:	
Center: (')	(Use ' before value to center).
Right: (")	(Use " before value to right-justify).
Left: (^)	(Use ^ before value to left justify).
Editing:	
Insert Column:	
step 1. <arrow>	(Position cursor at column location).
step 2. /E I C	(/(E)dit (I)nsert (C)olumn).
Insert Row:	
step 1. <arrow>	(Position cursor at row location).
step 2. /E I R	(/(E)dit (I)nsert (R)ow).
Move a Block:	
step 1. <arrow>	(Position cursor at upper left corner of column).
step 2. /E M	(/(E)dit (M)ove).
step 3. <.> <arrow>	(Place a . to anchor cursor and shade entire block to be moved).
step 4. <arrow>	(Move cursor to upper left corner of destination block. Warning! this procedure will overwrite the previous contents of the destination block).
Copy a Block	
step 1. <arrow>	(Position cursor at upper left corner of column).
step 2. /E C	(/(E)dit (C)opy).
step 3. <.> <arrow>	(Place a . to anchor cursor and shade entire block to be moved).
step 4. <arrow>	(Move cursor to upper left corner of destination block.
step 5. <enter>	(Push enter. Warning! this procedure will overwrite the previous contents of the destination block).
Delete a Column:	
step 1. <arrow>	(Move cursor to column to be deleted).
step 2. /E D C	(/(E)dit (D)elete (C)olumn).
step 3. <enter>	(Push enter. Warning! this procedure will delete all cells in this column for the entire spreadsheet!).

Delete a Row:

step 1. <arrow> (Move cursor to row to be deleted).
step 2. /E D R (/(E)dit (D)elete (C)olumn).
step 3. <enter> (Push enter. Warning! this procedure will delete all cells in this row for the entire spreadsheet!).

Moving a Block:

step 1. <arrow> (Position cursor at upper left corner of column).
step 2. /E C (/(E)dit (M)ove).
step 3. <.> <arrow> (Place a . to anchor cursor and shade entire block to be moved).
step 4. <arrow> (Move cursor to upper left corner of destination block.
step 5. <enter> (Push enter).

Lock headers:

Horizontal:

step 1. <arrow> (move cursor to just below header)
step 2. /W O L H (/(W)indows (O)ptions (L)ock Titles (H)orizontal).

Vertical:

step 1. <arrow> (move cursor to just beside header)
step 2. /W O L H (/(W)indows (O)ptions (L)ock Titles (V)ertical).

Clear:

step 1. /W O L C (/(W)indows (O)ptions (L)ock Titles (C)lear).

Divide a Matrix

step 1. (above) (same steps as above)
step 2. (reciprocal) (multiply 1st matrix by a single cell, the reciprocal of the number of columns).

Convert Matrix to Absolute Value:

step 1. (above) (same steps as above)
step 2. (1) (multiply 1st matrix by a single cell with a value of 1. Warning! cell contents generated by matrix math or summation functions should be multiplied by 1 as soon as possible to convert to absolute values, as cellular functions can easily assume new values.

Printing:

To Printer:

step 1. /P (/(P)rint - print command).
step 2. <Esc> (Escape - clears frozen field).
step 3. <arrow> (Move cursor to upper left corner of block to be printed).
step 4. <.> <arrow> (Enter a . to lock the position, then shade the block).
step 5. /D P (/(D)estination (P)rinter).

Printing:
To File:

step 1. (above)	(Same steps as above).
step 2. /D F	(/(D)estination (F)ile - sends output to a file).
step 3. <dir:\ filename)	(Specify directory and filename as output. Note: Quattro Pro adds a .prn extension to indicate an ASCII).

Retrieve Other Files:

step 1. /F C	(/(F)ile (C)lose).
step 2. Lose Changes?	(Yes - if no editing was done).
step 3. /F O	(/(F)ile (O)pen)
step 4. Select file.	(Select a file from the directory).

Appendix D

Procedure for using the Forage Allocation Model

Initiation:

step 1. cd\qpro	(DOS command - change to Quattro Pro directory)
step 2. q	(Keyword - invokes Quattro Pro)
step 3. /F D	(/(F)ile (D)irectory - changes file directory)
step 4. a:	(New directory = a:, allows storage of data on disk)
step 5. /F R	(/(F)ile (R)etrieve - retrieves file in a: directory)
step 6. <arrow>	(Move arrow to filename: FORTEST.WQ1. Note: do not use FORALL.WQ1 as this is the original copy; and always abandon FORTEST.WQ1 after each use.

EXTRA!

Optimization Start:

step 1. /TAO	(/(T)ools (A)dvanced math (O)ptimization - invokes the optimization function).
step 2. (subdirectory)	(For each item in the optimization menu, except for those noted, do the following:
a) <enter>	(Place cursor on item and press enter)
b) <arrow>	(Move cursor with arrow keys to the upper left hand corner of the block containing each item)
c) <.>	(Place a . in that cell to anchor the block)
d) <arrow>	(Move cursor with arrow keys to the right and then down to shade the block)
e) <enter>	(Define the block after shading by pressing <enter>; the block address then appears in the optimization menu)

The next 9 items in the optimization menu are:

1. Linear constraint coefficients - Matrix of coefficients of each decision variable (ungulate species). Coefficients are obtained by multiplying forage intake (6 months) by percent diet composition for each forage species/category.
2. Inequality/equality relations - Mathematical relationships (greater than or equal, equal to, or less than or equal) between the linear constraint coefficients and the constant constrain terms (below) for each forage species/category.
3. Constant constraint terms - (Limits) - A constant value of the availability of a forage species. Obtained by multiplying the estimated production of a forage species/category for each habitat type by the hectarage of that habitat and by an Allowable Use Factor of 0.35. Then production in all habitat types is summed for the entire Park.
4. Bounds for variables - Upper or Lower Bounds placed on ungulate numbers, restricting them to exceed or fall below a specified level.
5. Formula constraints - Ignore.
6. Objective function - The weighting given to each ungulate species. A value of 1 is generally input when ungulate species are to be weighted evenly.
7. Extremum (Largest) - Type of Problem Maximization (Largest, the one used in the forage allocation model) or Minimization (Smallest).
8. Solution - The single cell containing the total number of ungulates.
9. Variables - Ignore. Cells containing number of different ungulates.

10. Dual values - A sensitivity analysis for constant constraint terms (forage production). The amount by which the optimal value (solution) of the objective function would be increased or decreased if the limiting constant constraint term was raised by 1. Positive values indicate the constraint is limiting the solution; the highest value is most limiting. Negative values mean the constraint is in excess.
11. Additional dual values - A sensitivity analysis for the upper or lower bounds (whichever one is limiting the solution) of each decision variable (ungulate species). The amount by which the optimal value (solution) of the objective function would be increased or decreased if the limiting constant constraint term was raised by 1. Positive values indicate the constraint is limiting the solution; the highest value is most limiting. Negative values mean the constraint is in excess.

After items 1-4, 6-8, and 10-11 have been defined go to the next series of steps.

Optimization Run:

step 1. Go	(Push Go of the optimization Menu - Quattro Pro will now make an optimization run. If the run was feasible and a solution was obtained go to Change Parameters section below)
step 2. Infeasible	(Run was infeasible i.e. a solution was not possible, go to step 3.)
step 3. /EM	(/(E)dit (M)ove - move the entire line of the limting forage species (including: linear constraint coefficients; inequality/equality relations; constant constraint terms; and dual values) below the optimization problem work space.
step 4. /EDR	(/(E)dit (D)elete (R)ow - delete the now empty row in the optimization problem work space.
step 5. Go	(Rerun the problem, Quattro Pro has automatically adjusted the block size for each item in the menu).

Change Parameters:

Readjust any optimization parameters (including: linear constraint coefficients; inequality/equality relations; constant constraint terms; bounds for variables; or objective function and rerun problem.

Finish Modeling:

If one wishes to reset all block sizes of items in the optimization menu press <Reset>.

step 1. <Quit>	(Press quit to finish with model).
step 2. /FE	(/(F)ile (E)xit - exit Quattro Pro.
step 3. Lose Changes?	(<Yes> - Quattro Pro will abandon the file you were working in and retain the former copy. Note: always abandon the present file; do not retain the copy!).

Appendix E

Table 17. Abbreviations of all plant species names and species groups.

Abbreviation	Species/Species Group	Common Name
Graminoids		
Ag spp	*Agropyron* species	Wheatgrasses
Bo spp	*Bouteloua* species	Grama
Br spp	*Bromus* species	Brome
Ca spp	*Carex* species	Sedges
El spp	*Elymus* species	Wild-rye
Kopy	*Koeleria pyramidata*	Prairie Junegrass
Po spp	*Poa* species	Bluegrass
Scsc	*Schizachyrium scoparium*	Little Blustem
Stco	*Stipa comata*	Needle-and-Thread Grass
Stvi	*Stipa viridula*	Porcupine Grass
Grasstot	Total Graminoids	
Forbs		
Forbstot	Total Forbs	
Browse		
Amal	*Amelanchier alnifolia*	Juneberry, Serviceberry
Arca	*Artemisia cana*	Silver Sagebrush
Ardr	*Artemisia dracunculus*	Silky Wormwood
Arfr	*Artemisia frigida*	Fringed Sage
Arlu	*Artemisia ludoviciana*	White Sage
Artr	*Artemisia tridentata*	Big Sagebrush
At spp	*Atriplex* species	Saltbush, Silverscale
Chna	*Chrysothamnus nauseosus*	Rabbit Brush
Clli	*Clematis ligusticifolia*	Western Virgin's Bower
Eula	*Eurotia lanata*	Winter Fat, Winterfat
Frpe	*Fraxinus pennsylvanica*	Green Ash
Gusa	*Gutierrezia sarothrae*	Broomweed
Juco	*Juniperus communis*	Dwarf Juniper
Juho	*Juniperus horizontalis*	Creeping Juniper
Jusc	*Juniperus scopulorum*	Rocky Mountain Juniper
Prvi	*Prunus virginiana*	Chokecherry
Rhtr	*Rhus trilobata*	Skunkbush Sumac
Ri spp	*Ribes* species	Currant, Gooseberry
Ro spp	*Rosa* species	Wild Rose
Sh spp	*Shepherdia* speices	Buffaloberry
Sy spp	*Symphoricarpos* species	Snowberry, Wolfberry
Tora	*Toxicodendron radicans*	Poison Ivy
Yugl	*Yucca glauca*	Yucca
Browstot	Total Browse	