Carrying Capacity of Sympatric Ungulates in Central Alberta

University of Alberta

By

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Abstract

Dry matter intake (DMI) was estimated for mule deer (*Odocoileus hemionus*), wapiti (*Cervus elaphus*) and bison (*Bison bison americanus*) during paddock-level experiments and then incorporated into a forage allocation model to estimate optimal stocking combinations for the ungulate community in Elk Island National Park, Alberta. An inert chemical marker (*n*-alkane) was used to determine DMI and this was compared to the behavioral (bite-count) technique for mule deer, a species with broad diet selection. Calculations from pairing *n*-alkanes provided estimates of DMI that ranged from 1.29 - 2.73 kg/d. The *n*-alkane ratio technique was also used to determine animal-unit equivalence of mule deer, wapiti and bison. DMI of bison (11 kg/d), wapiti (6.9 kg/d) and mule deer (2.7 kg/d) differed significantly among species when expressed as total intake and percent body mass, but was similar when expressed as metabolic mass (92-124 g/kg/d $BM^{0.75}$). DMI related to metabolic mass did not differ between bison and mule deer in any comparison despite a 6.8-fold difference in body size, suggesting that intake scaled to metabolic mass. Linear programming was used to explore optimal combinations of bison, moose (*Alces alces*), wapiti and deer to maximize ungulate numbers and biomass when constrained by forage availability and genetically minimum viable populations (MVP) of bison and wapiti. Estimations for maximum numbers of animals produced a system dominated by deer and bison, which differed from estimations for maximum biomass in which bison and moose were abundant but deer were not present. Wapiti remained at MVP during all solutions. The input values of forage use (7-11%) provided optimal solutions consistent with current ungulate densities and are less than normally assumed for sustainable forage use, but reflect the need to incorporate other

biotic and abiotic losses to forage in carrying capacity models for which ungulate densities can be constrained by availability of a preferred forage class (e.g., grass) as well as forage quality. This research extends the conventional animal-unit concept to an animal-unit-year approach for annual estimates of carrying capacity for multi-species systems and provides a template based on forage biomass allocation for resource managers.

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Most of the mule deer, wapiti and bison I worked with carried cumbersome GPS radiocollars. Over the years, I have assisted in collaring hundreds of ungulates and have since become very sensitive their use. I sincerely hope information gained from these ungulates that carried these uncomfortable radiocollars is justified, and will reduce the need to collar other ungulates in the future.

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Chapter 1. Introduction

Wild ungulates are major ecological drivers in many ecosystems throughout the world (Barnes et al. 1999; Gordon et al. 2004; Edenius and Göran 2007; Moe and Wegge 2008) and provide resources to humans such as food and economic assets (van der Waal and Decker 2000; Leader-Williams et al. 2001; Loibooki et al. 2002). In a predator-prey system, ungulates are crucial to the survival of other animals such as large carnivores (Bodendorfer et al. 2006; Owen-Smith and Mills 2008) and consequently are a major part of shaping the evolution and dynamics of ecosystems (Andheria et al. 2007; Suzuki et al. 2008). In addition, the structure and function of ecosystems can be altered by ungulates (Pellerin et al. 2006; Manier and Hobbs 2007; Goheen et al. 2007) thereby influencing trophic relationships (Hebblewhite et al. 2005; Ripple and Beschta 2006; Beyer et al. 2007). In the absence of predation and hunting, ungulates are limited by food supply and their plentiful numbers can create management concerns (Saether 1997; Reyna-Hurtado and Tanner 2007; van Aarde and Jackson 2007).

In areas where ungulates thrive in human dominated landscapes, such as deer in North America (Stockton et al. 2005; Killmaster et al. 2007), Britain (Putman and Moore 1998), and Australia (Hall and Gill 2005) complex management challenges are presented because of conflicting human perceptions of ungulate management (Malo et al. 2004; Boehm et al. 2007). As human settlement continues to expand (Hardin 1971; Stokad 2005), less land remains available for those ungulates that require large and wild spaces (Chapin et al. 2000; Donlan et al. 2005; Butler et al. 2007). This has created conditions where some ungulates face conservation concerns due to low numbers or loss of habitat (Bodmer et al. 1988; Milner-Gulland et al. 2001; Coltman et al. 2003; IUCN 2007) and special management is required to maintain their existence (Cassinello et al. 2001; du Toit 2002). Surprisingly, some ungulate species considered abundant today have experienced extensive range reductions. For example, wapiti are thought to be the large mammal species (> 20 kg) with the greatest absolute range reduction since 1500AD, well ahead of other species such as the African elephant (*Loxodonta africana*), black rhinoceros (*Diceros bicornis*), caribou (*Rangifer tarandus*), and American bison (Morrison et al. 2007).

Because ungulates are large, they require substantial tracts of land to acquire adequate food resources (McNaughton et al. 1997; Pettorelli et al. 2003) and space to maintain their survival (Moe et al. 2007; Bergeron et al. 2008) and reproduction (Mysterud et al. 2002; Toïgo et al. 2007). Availability of vegetation, water, and shelter along with behavioral attributes such as gregariousness, can alter ungulate movements (Alder et al. 2001; Anderson et al. 2007; Chamaille-Jammes et al. 2007). By considering the distribution of ungulates and their varied resource needs, it becomes apparent that estimating the density of ungulates relative to impacts on vegetation can be challenging (Clutton-Brock et al. 2002; Albon et al. 2007).

Carrying capacity is one concept used to examine relationships between ungulates and vegetation (Leopold 1933; van Oene et al. 1999; Nugent et al. 2001). However, a precise and generally accepted definition of carrying capacity is often lacking which adds confusion to the concept (McNab 1985; Miller and Wentworth 2000), and carrying capacity has been used in different ways in different disciplines (Leopold 1933; Odum 1953; Hardin 1968; Ehrlich 1972; Caughley 1970; Wilson 1998). One could speculate that the complexity of measuring and implementing carrying capacity (McNabb 1985;

Morris and Mukherjee 2007) lies with the genesis of the concept itself (i.e., how much cargo a ship could carry, hence its carrying capacity) (Sayre 2007). This concept was first applied to the natural world to describe hunters that were limited by carrying capacity, meaning literally the number of animals the hunters could carry (Gabb 1873) and later used to describe the capacity of bees to carry pollen on their legs (Robertson 1887). This terminology was also applied to ranching practices to define the maximum number of livestock a rangeland could carry over time (Moore 1913; Stoddart and Smith 1955) and then later came to be used in wildlife management to describe the number of ungulates an area could sustain (Forbes and Overholts 1931; Leopold 1933; Edwards and Fowle 1955).

The concept of carrying capacity reverberated throughout Aldo Leopold's work in developing the discipline of wildlife management (Leopold 1933). By careful observation and use of available scientific information, he believed that overstocking a range with game birds would have no effect on future carrying capacity for the species, but conversely overstocking of browsing animals would have serious consequences. For example, in 1905 in the Kaibab plateau of the Grand Canyon, when hunting was banned and predators were eliminated, the mule deer increased in numbers and outstripped their food supply, causing a population crash through starvation (Leopold 1933).

Similarly, ecologists have used carrying capacity to describe human population growth in relation to the available resources on the planet (Odum 1953; Woodbury 1955). On the eve of World War two, Leopold (1941) wrote a philosophical essay using an analogy of animal population growth with that of humans, and pondered about a moratorium on human population growth, to reduce the carrying capacity and subsequent stressors on the planet. There is still much debate about the carrying capacity of the planet and whether it has already been exceeded (Hardin 1986; Ehrlich and Ehrlich 1990), but others remain more optimistic with initiatives such as sustainable agriculture (Bhutto and Bazmi 2007; Pretty 2008) and ecologically sustainable development (Termorshuizen et al. 2007; McMichael 2008). With the world population currently growing at rates of greater than 200,000 people per day (World Health Organization 2007), some are questioning why there is such disharmony between science and society when dealing with a carrying capacity problem that appears so obvious to many (Cao et al. 2007; Ehrlich 2008). For wildlife ecologists, this issue was briefly addressed in 1993 at the North American Wildlife and Natural Resource conference during one session titled: Human Population – The Unblamed Factor. Ten papers were presented, but only vague reference was made (Coleman 1993) to reducing human population to benefit wildlife (Bolen and Robinson 2003). Some wildlife ecologists are trying to link increased human impact on the environment by monitoring animal numbers in relation to sustainability of vegetation (Wood et al. 2008).

In wildlife and range science the definition of carrying capacity falls under two broad categories: ecologically based carrying capacities used by population biologists (Caughley 1979; McCullough 1999; Halpern and Underwood 2006) and culturally based carrying capacities used by range scientists (Caughley 1979; Westoby 1980; Dhondt 1988; Holechek et al. 2004; Miller and Wentworth 2000). Caughley (1979) offered one definition of carrying capacity within each of these two general categories. He described ecological carrying capacity as an equilibrium between plants and herbivores in an unmanipulated system, and economic carrying capacity (culturally based) as an equilibrium between plants and herbivores, but with a sustainable limit imposed on the number of herbivores to achieve a prescribed forage use (Caughley 1979).

Ecological carrying capacity is attained when ungulate densities increase over time to a point where they are in equilibrium with their food supply. At equilibrium, the growth rate of the herbivore population is zero. When herbivores are at equilibrium, the numbers of births minus the number of deaths equals zero because competition for food supply will theoretically lead to increased juvenile and adult mortality rates, and depressed reproductive rates with advanced age of sexual maturity. In a new system, herbivore populations may increase beyond carrying capacity before equilibrium is reached, and the herbivores may negatively affect vegetation, and thus their numbers will decline. This system of an initial irruption of herbivore numbers, followed by decline, and subsequent damped oscillations in both herbivore and plant abundance is thought to be the normal pattern in ungulate populations in new environments (Caughley 1970; Rooney and Waller 2003; Forsyth and Caley 2006; White et al. 2007).

Conversely, economic carrying capacity is defined as an ungulate population controlled by humans at levels below ecological carrying capacity (Caughley 1979; McCullough 1992). Range mangers seek to maximize animal productivity while maintaining sustainable range condition (Stoddart and Smith 1955; Westoby 1980; Dhondt 1988; Holechek et al. 2004). With this form of sustainable forage use, the density of ungulates will normally remove 35-50% of the available forage biomass (Irby et al. 2002; Holechek et al. 2004).

Carrying capacity is rarely estimated in ecological field studies (Morris and Mukherjee 2007) mostly because of difficulties gathering the required information (Miller and Wentworth 2000). Dry matter intake (DMI) is a required parameter for carrying capacity estimates for ungulates, but attaining DMI rates has been hampered by a lack of an effective technique that can be reliably conducted concurrently on several animals. To address this deficiency, I used inert chemical markers (*n*-alkanes) as an innovative method (Mayes et al. 1986; Smith and Strickland 2007; Barcia et al. 2007) to refine DMI estimates for mule deer (Chapter 2). I chose mule deer for this research because of their broad diet selection, which makes determining their dry matter intake (DMI) challenging, and I assumed if the *n*-alkane technique could be used successfully to estimate DMI for mule deer (Kuzyk and Hudson 2006), it could be used with other species such as bison having less complex diets. Also, since traditional techniques used to estimate DMI are labor-intensive, I assumed the *n*-alkane technique could be used as a novel technique to estimate DMI concurrently for multiple species (Chapter 3).

As most systems contain multiple species of ungulates, concurrent estimates of DMI for sympatric ungulates are required for carrying capacity estimates. Because DMI estimates for multi-species systems are rare (Holechek et al. 2004), I used the *n*-alkane technique to estimate DMI for sympatric mule deer, wapiti and bison (Chapter 3). I tested assumptions of the animal-unit concept where DMI equates to 2-3% of an ungulate's body mass (Stoddart and Smith 1955; Holechek et al. 2004), by comparing them to intakes related to metabolic mass (Kleiber 1947; Ostrowski et al. 2006). I predicted that mule deer, wapiti and bison would consume the equivalent of 2-3% of their body mass per day (or roughly 10% of their metabolic mass per day), and this would not differ among the three species. I also developed the temporal component of the animal-unit concept by extending daily intakes to animal-unit-months. Once intakes were standardized among three species (Kuzyk and Hudson 2007), the next step for a carrying capacity estimate was to advance the animal-unit-month to seasonal and annual time steps (Chapter 4).

Management decisions for wild ungulates are normally made on an annual basis (du Toit 2002; Gordon et al. 2004; Morellet et al. 2007). Therefore, I developed an annual estimate of carrying capacity for a multi-species system using a forage allocation approach. I did this by incorporating DMI estimates gathered during paddock-level experiments (Chapter 2 and 3) into an annual carrying capacity estimate for four species (Chapter 4). I used an elaboration of the animal-unit concept by extending the animal-unit-month to an animal-unit-year. I used Elk Island National Park as a case study for estimating annual carrying capacity because it contains four ungulate species and presents real management concerns for a park that is enclosed by a fence and lacks predators. In Chapter 5, I discuss the contributions of this research to furthering our understanding and means of implementing carrying capacity for multi-species ungulate systems.

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Chapter 2. Using *n*-Alkane Markers to Estimate Forage Intake of Mule Deer

2.1 Introduction

Mule deer exist over much of western North America and can be viewed as keystone species by altering vegetation composition (McArthur et al. 1988; Hanley 1996) and affecting ecosystem processes (Hobbs 1996). Despite their ecological importance, little is known about trophic dynamics of mule deer, with studies largely limited to central and southern parts of their range (Alldredge et al. 1974; Collins and Urness 1983; Wickstrom et al. 1984). Beyond diet selection, forage intake is the most important parameter for determining relationships of mule deer to their environment, especially on northern ranges where strong seasonal cycles alter vegetation quality and quantity and thus affect potential mule deer ingestion.

Accurate estimates of forage intake by mule deer are difficult to obtain. Fallout cesium-137 requires sampling large numbers of mule deer carcasses (Alldredge et al. 1974). Studies using oesphageally-fistulated animals typically involve few individuals (Wickstrom et al. 1984). Monitoring the behaviour of tame free-ranging mule deer can provide estimates of intake (Collins and Urness 1983) but there is a large time investment required to raise and condition the research animals. Observational techniques used to estimate daily dry matter intake (DMI) in cervids (Hudson and Watkins 1986) may be inaccurate and usually lead to overestimates of intake when compared with other marker techniques (Jiang and Hudson 1992; Gedir and Hudson 2000b). Most marker techniques require daily or twice daily dosing that can interrupt

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ungulate feeding patterns (Jiang and Hudson 1992) but slow release markers from an intra-ruminal controlled-release device (CRD) alleviate these constraints (Laby 1981; Ellis et al. 1981).

Long chain *n*-alkanes found in natural vegetation have been used in combination with orally-dosed synthetic *n*-alkanes released from a CRD to estimate forage intake of domestic ruminants (Mayes et al. 1986). This paired-marker technique uses faecal recovery of odd-chained *n*-alkanes (C_{31} or C_{33}) found in plant cuticular wax with even-chained synthetic *n*-alkane (C_{32}) delivered at a constant rate from the CRD. Recovery of *n*-alkanes is incomplete owing to their minimal digestibility by ruminants but odd and even-chained *n*-alkanes have similar recovery rates and thus can be used to estimate forage intake (Dove et al. 2002). *n*-Alkane markers have been used to estimate DMI of domestic ungulates (Mayes and Dove 2000), red deer (*Cervus elaphus elaphus*) (Heydon et al. 1993), wapiti (Gedir and Hudson 2000a) and fallow deer (*Dama dama*) (Ru et al. 2002) but have not been tested in Odocoileinae deer. Estimating intake in deer is challenging because browse in their diets contain large quantities of *n*-alkanes (Gedir and Hudson 2000b; Bugalho et al. 2005), which means diet composition must be known. Because of untested methodology and complexity of mule deer diets, DMI estimates should be calibrated using several methods. The objective of this study was to (i) evaluate *n*-alkane markers as a technique to estimate forage intake of free-ranging mule deer, (ii) compare estimates of forage intake using the *n*-alkane marker and bite count methods, and (iii) assess seasonal and annual foraging parameters of mule deer grazing in tandem (mule deer only) and mixed (mule deer, wapiti, bison) assemblages.

2.2 Materials and Methods

2.2.1 Study Area

This study was conducted at the University of Alberta Ranch (53° N and 111° 31' W) approximately 150 kilometers southeast of Edmonton, Alberta, Canada. The elevation is 705 meters above sea level with climate characterized by short warm summers and long cold winters with average temperatures of 17°C in July and -12°C in December (Environment Canada 2006). The area is classed as aspen parkland (Strong 1992) with stands of trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*) interspersed with grassland and shrubland. Forest understory and ecotones contain rose (*Rosa* spp.), raspberry (*Rubus idaeus*), Canadian gooseberry (*Ribes oxyacanthoides*), Saskatoon (*Amelanchier alnifolia*) and snowberry (*Symphoricarpos albus*). Grasslands are comprised of rough fescue (*Festuca halli*), smooth brome (*Bromus inermis*), bluegrass (*Poa pratensis*), blue grama (*Bouteloua gracilis*) and a variety of forbs such as strawberry (*Fragaria* spp.) and asters (*Aster* spp.). There are semi-permanent water bodies surrounded by willow (*Salix* spp.), aquatic sedges (*Carex* spp.), and dandelions (*Taraxacum officinale*).

2.2.2 Experimental Design and Animals

This experiment was part of a larger study using mixed and tandem assemblages of ungulates (Table 2-1). Mixed assemblages contained mule deer, wapiti and bison together in paddocks for 45 days. Tandem assemblages contained only one of three ungulate species (mule deer, wapiti or bison), which were rotated through the same paddock on 15-day intervals (Table 2-1). Both mixed and tandem assemblages had three concurrent replications. Ungulates were contained within separate 4 to 8-ha fenced paddocks containing similar, but varying amounts of vegetation (Didkowsky 2006). One or two mule deer in each paddock were instrumented with radiocollars (Telonics TGW-3570, GPS/VHF) to allow rapid location of focal animals. All research was conducted through the University of Alberta and approved by the Faculty Animal Policy and Welfare Committee (Protocol HUDS 2004–33B), following guidelines of the Canadian Council on Animal Care.

Seven grazing trials (15 days each) were conducted in 2004 and 2005 to assess foraging parameters of tractable mule deer with four of the seven trials (Sept/04, June/05, July/05, Sept/05) including the *n*-alkane marker technique. The trials in 2004 took place in the first 15 days of July, September and October with the 2005 trials conducted the first 15 days of June, July, September and October. These sampling intervals were chosen because they corresponded to the main vegetation phenological stages: fully green (June and July), maturing (September) and fully cured (October).

Eleven adult female mule deer (tame and non-tame) were used during the *n*-alkane marker trials. They were non-lactating, of mean age 4.8 ± 2.1 years (mean ± SD) and weighed 60.1 ± 5.8 kg (mean ± SD). Only four of the study animals could be used in all trials (*n*-alkane marker and bite count methods) as they were fully habituated to human presence and allowed undisturbed observations of foraging activities at less than five meters. Using tame deer to study foraging parameters is deemed reliable because food intake is considered innate (Spalinger et al. 1997). The four tame deer were always in separate paddocks, with two deer in separate tandem paddocks and two deer in separate mixed paddocks. Mule deer were weighed at the beginning and end of each 15-

day trial. Calculations for metabolic mass (g/kg BM $^{0.75}$) were standardized by using mass taken at the beginning of each 45-day trial (June 1 and September 1), as trial lengths varied between mixed and tandem paddocks (Table 2-1).

2.2.3 Administering *n*-Alkane Capsules and Calculations

At the beginning of each *n*-alkane trial, one CRD designed for domestic sheep (Captec ©™) was administered orally with a dosing-gun (Captec ©™) into the rumen of a mule deer. Twenty-three *n*-alkane capsules were given to 11 deer with each deer receiving between one to four capsules during the study. The manufacturer (Captec ©™) had specified release rates of 50 mg C_{32}/day for 20 days, after which time the release rate is unknown and variable. But Ru et al. (2002) found that release rates using the same capsules in fallow deer were 40 mg C_{32}/day, possibly due to the rumen motility of deer. This finding is similar to Dove et al. (1991), where release rates for domestic sheep were 41.7 mg C_{32}/day. Therefore, our calculation of DMI followed Ru et al. (2002). *n*-Alkane concentrations were determined from freshly voided faecal pellets collected 7-10 days after commencement of the trial, giving the dosed *n*-alkanes time to achieve steady state.

Focal animals were followed until one to four samples of freshly voided fecal pellets were collected. The pellets were handled with rubber gloves, sealed in plastic bags and placed in a deep freeze within 6 h of collection. Vegetation samples for *n*-alkane analysis were gathered concurrently using the simulated-bite technique (bite rate x bite size x foraging time) (Hudson and Watkins 1986). Vegetation samples from tame deer in the same or adjacent paddocks were used for calculating DMI for the seven non-tame deer. All vegetation samples gathered during bite counts were pooled for individual deer and each time period and then analysed for *n*-alkane concentrations. In September 2004, plant parts from six pasture plants commonly consumed by mule deer were gathered to test for *n*-alkane concentrations among plant species. Analysis for *n*-alkane concentrations was conducted at the Department of Animal Science, University of Manitoba following Moshtaghi Nia and Wittenberg (2002) and Boadi et al. (2002). Updates to this method include using a gas chromatograph (Varian 3900) having a fused capillary column (30m x 0.32cm x 0.25 *u*m film) and a run time of 18 min with He as the carrier gas.

DMI was calculated by pairing C_{32} with C_{31} or C_{33} using the following formula outlined in Gedir and Hudson (2000a):

$$\text{DMI (kg/day)} = (D_{32} \times Fn/F_{32}) / [Hn - (Fn/ F_{32}) \times H_{32}]$$

where D_{32} is the excretion rate of C_{32} (mg/day), F_{32} and H_{32} are concentrations (mg/kg DM) of C_{32} in the recovered faecal sample and vegetation, respectively, and Fn and Hn are respective concentrations (mg/kg DM) of natural odd-chained *n*-alkanes (C_{31} or C_{33}) found in the faeces and vegetation.

2.2.4 Bite Count Method

Foraging behaviour was studied using bite rates (bites/min), bite size (mg/bite) and consumption rates (g/min) following a protocol used in similar studies for wapiti (Hudson and Nietfeld 1985; Gedir and Hudson 2000), moose (Renecker and Hudson 1986) and bison (Hudson and Frank 1987). These studies aimed to determine the various factors affecting instantaneous intake rates but it is theoretically possible to determine daily totals if grazing time is accurately recorded.

Bite rates of individual mule deer were recorded on a mechanical counter during 5 min intervals (Wickstrom et al. 1984) and alternated with 5 min of non-monitoring to account for random movements. Monitoring was abandoned if the mule deer spent less than 50% of the sampling interval (2.5 min) engaged in foraging and pursued other activities such as bedding, interacting with other animals, or walking to different habitats. Each deer was observed for about 15 (range 3-25) five-min intervals during each of the study periods. Data were collected in the morning and afternoon (e.g., 7 in morning; 8 in afternoon) and pooled for each deer. Immediately following the bite rate sampling, 20 hand-plucked simulated bites were collected to represent the plants and plant parts selected by deer (Hudson and Nietfield 1985). Bite samples were oven-dried at 60°C for 48 h and then weighed on an electronic scale to attain bite size mass. Theoretical maximum intake rates were calculcated following Shipley and Spalinger (1992):

$$\text{Rmax} = 0.662 \text{ X } \text{BM}^{0.762}$$

where Rmax is the theoretical maximum intake rate (g/min), 0.662 is a constant, and $\text{BM}^{0.762}$ is body mass scaled to occlusal area of the molars.

2.2.5 Activity Budgets

Activity budgets were conducted using scan sampling (Altmann 1974) on one deer for 24 h in tandem paddocks during seven trials. The same individual was used for six trials, but was substituted during the last trial (October 2005) to test for consistency of foraging times. Activity budgets consisted of one 24-h scan representing predominant activities of feeding, bedding, walking and other (grooming, social interactions). The focal animal was closely observed and the predominant activity recorded every 10 min. The activity was termed predominant if it occurred for 5 min or longer during the 10-min interval. During darkness, the focal animal was observed with a flashlight where the light beam concentrated on the posterior portion of the body to minimize disturbance (Appendix 1).

2.2.6 Statistical Analysis

Deer mass and ages are presented with standard deviations and all other analyses are given with standard errors. During the *n*-alkane marker trials, only some deer were used in all trials. Hence, a repeated measure Wilcoxon paired–sample test was used to maximize the number of statistical comparisons of DMI (Zar 1999). Means and standard errors of DMI are presented for all animals but statistical analysis is limited to comparing those individuals used in repeated trials.

Foraging rates (g/min) were computed by multiplying bite rate (g/min) by bite size (mg/bite). Because the same four deer were used to study all foraging parameters, a repeated measure ANOVA (Friedman Test) was used to compare foraging parameters and DMI bite count estimates between seasons and years. A Friedman test was also used to compare total *n*-alkane concentrations (C_{29}-C_{33}, C_{36}) among six pasture plants commonly consumed by mule deer. A Wilcoxon paired–sample test was used to determine pairwise comparisons following significant ANOVA results (Zar 1999). A Mann-Whitney U test was used to evaluate differences between DMI estimate techniques and to compare foraging parameters between mule deer in tandem and mixed paddocks. Simple linear regression was used to examine relationships between DMI estimate techniques. Statistical analyses was performed using SYSTAT (Version 11.0) and SPSS (Version 14.0) where all values with $p < 0.10$ were considered significant due to the few deer and small sample of pasture plants.

2.3 Results

2.3.1 Comparison of DMI with *n*-Alkane and Bite Count Methods

In three of 23 occasions (1 Sept/04, 1 June/05, 1 Sept/05) no synthetic *n*-alkane was found in faecal samples so these mule deer were presumed to have regurgitated the CRDs. Concentrations of *n*-alkanes (C_{29}-C_{33}, C_{36}) differed among six plants (Friedman test, $p = 0.02$) commonly consumed by mule deer (Table 2-2). Means and standard errors of all DMI estimates are presented for mule deer (tame and non-tame) used in *n*-alkane trials (Table 2-3). The only significant difference was with C_{31} between June 05 and Sept 05 (Wilcoxon paired–sample test, $p = 0.07$). DMI estimates (kg/day) did not differ using pooled seasons with C_{31} (Wilcoxon paired–sample test, $p = 0.16$) or C_{33} (Wilcoxon paired–sample test, $p = 0.46$) or between mule deer in mixed and tandem paddocks (Mann-Whitney U test, $p = 0.68$). DMI estimates (kg/day) did not differ between bite count and C_{31} (Mann-Whitney U test, $p = 0.23$) but there was some evidence that DMI estimates differed between bite count and C_{33} (Mann-Whitney U test, $p = 0.08$). There was no difference in DMI estimates between C_{31} and C_{33} (Mann-Whitney U test, $p = 0.53$) (Figure 2-1).

2.3.2 Foraging Parameters

Bite rates (bites/min) were greatest (26.6 bites/min) in July 2005 and lowest in

September 2005 (19.6 bites/min), with no difference found among seasonal periods in either 2004 (Friedman test, $p = 0.46$) or 2005 (Friedman test, $p = 0.55$). However, there were differences when all seven seasons were combined (Friedman test, $p = 0.04$) (Table 2-4). Maximum bite sizes (mg/bite) occurred in October 2005 (174.5 mg/bite), and were lowest in July 2004 (48.5 mg/bite), with differences among seasons in 2004 (Friedman test, $p < 0.001$) and 2005 (Friedman test, $p < 0.001$) and with all seasons combined (Friedman test, $p < 0.0001$). Consumption rates (g/min) were greatest in October 2005 (3.1 g/min), lowest in July 2004 (1.0 g/min), and differed between seasons in 2004 (Friedman test, $p < 0.001$) and 2005 (Friedman test, $p = 0.03$), and among the seven seasonal periods (Friedman test, $p < 0.0001$). Differences between years (pooled July, Sept, Oct of each year) existed for bite rate (Friedman test, $p = 0.07$), bite size (Friedman test, $p < 0.001$) and consumption rate (Friedman test, $p < 0.001$). When foraging parameters were analysed between the two deer in tandem versus the two deer in mixed paddocks, no differences were found in consumption rates (Mann-Whitney U test, $p = 0.58$), bite rates (Mann-Whitney U test, $p = 0.89$) or bite size (Mann-Whitney U test, $p = 0.66$). Intake rates (g/min) approached maximum (Rmax) on three occasions during this study (Table 2-5) and there was some evidence of a relationship between consumption rate and bite size ($r^2 = 0.47$) (Figure 2-2). Mule deer spent more time feeding during July (11.3 hrs/day) and the least time feeding in October (9.3 hrs/day). There was minimal disparity in feeding times among individual deer in October 2004 and October 2005 (Appendix 1).

2.4 Discussion

The double *n*-alkane ratio technique provided DMI estimates for mule deer consistent with values for other ungulates based on percent body mass (Holechek et al. 2004). The bite-count method gives greater estimates of DMI for wapiti when compared to marker methods (Jiang and Hudson 1992; Gedir and Hudson 2000b), but our results were generally contrary to these findings. Shrub content in the diets of mule deer had been estimated at 30-40% (Didkowsky 2006), and shrubs in this study area had variable concentration of *n*-alkanes, which could possibly affect DMI estimates. For example, rose can be a preferred food item of mule deer and had concentrations of C_{31} and C_{33} that were at least 4-5 times higher than other plant species. These findings are consistent with Dove et al. (1996) who found that plant species account for most variation in *n*-alkane concentration (85%) over plant parts or date of harvest. Wapiti prefer to feed on grass in summer and fall, which generally have consistent concentrations of *n*-alkanes (Gedir and Hudson 2000b). Previous studies found C_{33}:C_{32} to be a more accurate pairing than C_{31}:C_{32} (Gedir and Hudson 2000b) mostly due to a better recovery rate of *n*-alkanes as chain length increases (Dove and Mayes 1991), although in this study, there was no difference in DMI (kg/day) estimates based on *n*-alkane pairings.

Alldredge et al. (1974) determined the average annual food intake rate of mule deer to be 22 g of dry matter per kilogram of body mass, which equates to 1.5 kg/day for a 68-kg deer (Anderson and Wallmo 1984). Similar estimates were found with the bite count and *n*-alkane methods, as mule deer (60.1 ± 5.8 kg) consumed between 0.68 and 2.44 kg/day during summer and autumn. Our experimental animals were fed balanced rations during the winter, and were not lactating during the experiment, which could explain our lower levels of intake during summer. We found the greatest rates of DMI occurred in September and October, with values near 2 kg/day during both months. This increased intake could be a physiological response to store energy supplies for the November breeding season and upcoming winter. For example, Parker et al. (1999) found that black-tailed deer (*Odocoileus hemionus hemionus*) in coastal environments were in a negative energy balance throughout most of the winter.

Estimates of intake based on metabolic mass ranged from 14 - 40 g/kg BM$^{0.75}$ using the bite count method to 68 – 124 g/kg BM$^{0.75}$ with the *n*-alkane method (C_{31} and C_{33}). Values were generally greatest during autumn and lowest in summer and were similar to the 40-90 g/kg BM$^{0.75}$ reported by Collins and Urness (1983) for mule deer on summer ranges in Utah. Voluntary food intake of penned black-tailed deer was 67 g/kg BM$^{0.75}$ for non-lactating females, whereas females with single and twin fawns consumed 130% and 170% this rate, respectively (Sadleir 1982). Mule deer in this study were in paddocks and would have other energy expenditures during daily activities such as intra and interspecific interactions and dealing with weather variables. Mule deer would occasionally interrupt feeding when watching other ungulates within the fence or wild mule deer outside the fence and when listening to coyotes (*Canis latrans*) howling.

Foraging rates of ungulates can be limited by forage quality and forage quantity, and be related to plant density or bite size of plants (Spalinger et al. 1988; Gross et al. 1993). Empirical relationships have been established between feeding rate and plant biomass (Trudell and White 1981; Hudson and Nietfeld 1985), but theoretical considerations and empirical evidence suggest that feeding rate may not depend solely on biomass due to confounding effect of bite size, forage structure and spatial arrangement

(Spalinger et al. 1988; Laca et al. 1994; Fortin et al. 2004; Searle et al. 2005). Mean bite rates during summer were lower (21.7 – 26.6 bites/min) than those for two fistulated mule deer (27.4 - 45.5 bites/min) studied by Wickstrom et al. (1984), but bite size was higher in this study (49 – 93 mg/bite) compared to Wickstrom et al. (1984) (48 – 77 mg/bite). The difference may have been due to our estimates, or that the fistulated animals were fasted for 18 h before data collection and because many of these measurements were taken when the animals were feeding on grass. One difference from this study is the large bite sizes found during October (134 - 176 mg/bite), but no other temporal comparisons could be found in the literature.

Consumption rates of mule deer in aspen parkland habitats varied markedly over the summer and autumn seasons and between years. Consumption rates of mule deer in summer during this study (1.0 –2.5 g/min) were similar to those found for mule deer in Utah (1.8-3.3 g/min) (Collins and Urness 1983), in northeastern Oregon (2.1 – 3.7g/min) using fasted animals (Wickstrom et al. 1984), and for black-tailed deer in Alaska (~ 1.5 g/min) (Gillingham et al. 1997). Maximum intake rates in this study were found in October of both years (2.9 - 3.1 g/min), but no other studies involving mule deer provided seasonal comparisons.

Three of the four mule deer occasionally fed at rates (14.3 – 15.6 g/min) that approached the theoretical maxima (14.7 – 16.3 g/min) (Shipley and Spalinger 1992) and were well above the seasonal mean consumption rates of 2.8 g/min, and having all these events occur in October when consumption rates averaged 2.9 – 3.1 g/min. These maximum rates were mostly related to mule deer eating Canada thistle (*Cirsium arvense*). While eating thistle, the deer would often eat individual leaves and then break off the stalk several centimeters from its mouth, leaving the stalk protruding from the mouth while slowly ingesting the stalk. These foraging bouts were often interspersed with deer feeding rapidly on grass, as thistle and grass were regularly found together in heavily grazed areas. These two plants were normally the only remaining vegetation still green in October and were actively sought by mule deer. These findings are similar to coastal black-tailed deer feeding on skunk cabbage (*Lysichiton americanus*) (Gillingham et al. 1997). The difference in our study was that thistle was relatively rare and appeared to be eaten only after other vegetation had cured, whereas skunk cabbage was a relatively available food item for black-tailed deer.

There was no difference in any foraging parameter between the two mule deer in the mixed paddocks with bison and wapiti, and the two mule deer in the tandem paddocks (mule deer only). This may have been due to the small sample size of individuals to accurately test this assumption. It was uncommon to see mule deer stop foraging and move away from wapiti or bison, but on several occasions, mule deer would interrupt their feeding to socially interact with mule deer in their own paddocks, or with mule deer in adjacent paddocks. Within paddocks, what appeared to be a dominant mule deer would occasionally chase another group member, which often altered the foraging of the entire group. Mule deer would also interrupt feeding to investigate (smell) another mule deer across the fence and either walk the fence line adjacent to the mule deer, or at times run in unison with the other mule deer. These observations, combined with a lack of a significant relationship between paddock types, suggest that intraspecific relationships may be equally or more important for altering foraging rates of mule deer than interspecific interactions.

The *n*-alkane marker technique provided encouraging results for estimating DMI in mule deer. By comparing foraging parameters concurrently with *n*-alkane marker DMI estimates, a better understanding was gained of foraging relationships of mule deer in a northern habitat. DMI was greater in autumn than in summer with mule deer adjusting bite sizes to attain these higher rates in autumn. Canada thistle, which is often treated as an undesirable weed, appears to be an important food item for mule deer after other vegetation has cured, and allows them to achieve near theoretical maximum intake rates. The next step for using *n*-alkane markers to study DMI of mule deer should be to use animals outside an enclosure such as semi-tame mule deer in parks or urban environments. Possibly *n*-alkane capsules could be administered to wild mule deer and faecal and vegetation samples collected when following radiocollared animals.

Table 2-1. Group composition of mule deer, wapiti and bison in tandem (rotation of each species) and mixed (all species) assemblages at the University of Alberta Ranch, Kinsella, Alberta, in the summer and autumn of 2004 and 2005.

Trial Type	Mule Deer	Wapiti	Bison
		2004 (number of animals)	
Mixed (45 days)	2	2	2
Tandem (15 days each species: deer, wapiti, bison)	4	4	4
Tandem (15 days each species: bison, wapiti, deer)	4	4	4
		2005 (number of animals)	
Mixed (45 days)	2	3	3
Tandem (15 days each species: deer, wapiti, bison)	3	3	6
Tandem (15 days each species: bison, wapiti, deer)	3	3	6

Table 2-2. Comparison of total *n*-alkane concentration (mg/kg DM) of common plants consumed by mule deer in September/04 at University of Alberta Ranch, Kinsella, Alberta.

	C_{29}	C_{30}	C_{31}	C_{32}	C_{33}	C_{36}	Total
Aster [a]	83	17	263	29	120	13	525
Rose [a]	310	12	1286	17	808	4	2437
Aspen[b]	56	6	16	2	3	5	88
Gooseberry[b]	117	18	424	24	79	4	666
Snowberry [a]	524	16	307	2	10	4	863
Willow[c]	43	1	2	1	1	4	52

Note: Plants that share superscript do not differ in *n*-alkane concentrations ($p > 0.10$).

Table 2-3. Estimates of DMI (kg/d) derived from the *n*-alkane marker method for mule deer (n) on summer and autumn pastures (2004/05) at the University of Alberta Ranch, Kinsella, Alberta.

Mule Deer	Sept/04 (n = 5)	June/05 (n = 5)	July/05 (n = 3)	Sept/05 (n = 6)
DMI C_{31} (kg/day)	2.70 ± 0.2	2.13 ± 0.5	1.29 ± 0.2	2.54 ± 0.3
DMI C_{33} (kg/day)	2.71 ± 0.2	1.94 ± 0.6	1.43 ± 0.4	2.73± 0.4
DMI C_{31} (g/kg $BM^{0.75}$)	124 ± 8	99.6 ± 21	74.5 ± 10	112 ± 16
DMI C_{33} (g/kg $BM^{0.75}$)	124 ± 9	90.2 ± 26	67.9 ± 20	120 ± 20
Body Mass (kg)	60.9 ± 3	59.4 ± 2	57.2 ± 1	65.3 ± 2

Note: Values are means ± 1 SE.

Table 2-4. Seasonal foraging rates of mule deer (n = 4) derived from the bite-count method on summer and autumn pastures at the University of Alberta Ranch, Kinsella, Alberta.

	Jun-05	Jul-04	Jul-05	Sep-04	Sep-05	Oct-04	Oct-05	p value
Bite rates (bites/min)	20.6^{b}	21.7^{bc}	26.6^{a}	22.3^{bc}	19.6^{bc}	22.4^{c}	22.2^{abc}	**0.04**
Bite size (mg/bite)	97.0^{a}	48.5^{b}	92.7^{a}	118.5^{c}	130.3^{d}	134.0^{de}	174.5^{e}	**0.0001**
Consumption rates (g/min)	2.1^{a}	1.0^{b}	2.3^{c}	2.5^{ac}	2.8^{cd}	2.9^{de}	3.1^{e}	**0.0001**
DMI bite count (kg/d)	1.3^{a}	0.6^{b}	1.6^{c}	1.6^{c}	1.8^{c}	1.7^{c}	1.7^{c}	**0.0001**
DMI bite count (g/kg $BM^{0.75}$)	28.0^{a}	13.9^{b}	35.1^{c}	36.9^{c}	40.7^{c}	38.1^{c}	40.1^{d}	**0.0001**

Within a row, medians with the same letter do not differ ($p > 0.10$).

Table 2-5. Theoretical maximum intake rates (Rmax = 0.662 X BM $^{0.76}$) of mule deer (n = 4) compared to seasonal field estimates at the University of Alberta Ranch, Kinsella, Alberta.

Deer	Theoretical Rmax (g/min)	July 15/04 (g/min)	Sept1/04 (g/min)	Oct 15/04 (g/min)	June1/05 (g/min)	July 15/05 (g/min)	Sept1/05 (g/min)	Oct 15/05 (g/min)
501H	15.35	0.98 (0.18-3.13)	3.00 (0.52 - 7.17)	2.65 (0.67-14.49)	2.77 (0.53 - 5.47)	2.90 (1.26 - 4.49)	3.39 (0.83 - 6.79)	4.82 (1.39 - 5.90)
502H	15.84	1.16 (0.98 - 1.51)	2.52 (0.83 - 4.50)	2.54 (1.23 - 5.95)	2.18 (1.26 - 2.97)	2.55 (0.88 - 4.96)	3.20 (1.06 - 8.79)	3.31 (0.93 - 4.28)
504H	16.30	1.50 (0.35 - 4.88)	2.20 (1.05 - 4.32)	4.81 (1.32 - 7.89)	2.27 (1.57 - 3.18)	2.96 (0.84 - 6.85)	2.56 (1.12 - 4.43)	2.63 (1.10-15.57)
515K	14.67	0.91 (0.26 - 1.37)	2.81 (1.52 - 5.38)	4.44 (1.68-14.27)	1.60 (0.69 - 3.00)	2.48 (1.21 - 5.51)	2.97 (1.04 - 5.02)	6.99 (1.22 - 6.92)

Note: Calculations for Rmax used mean mass of

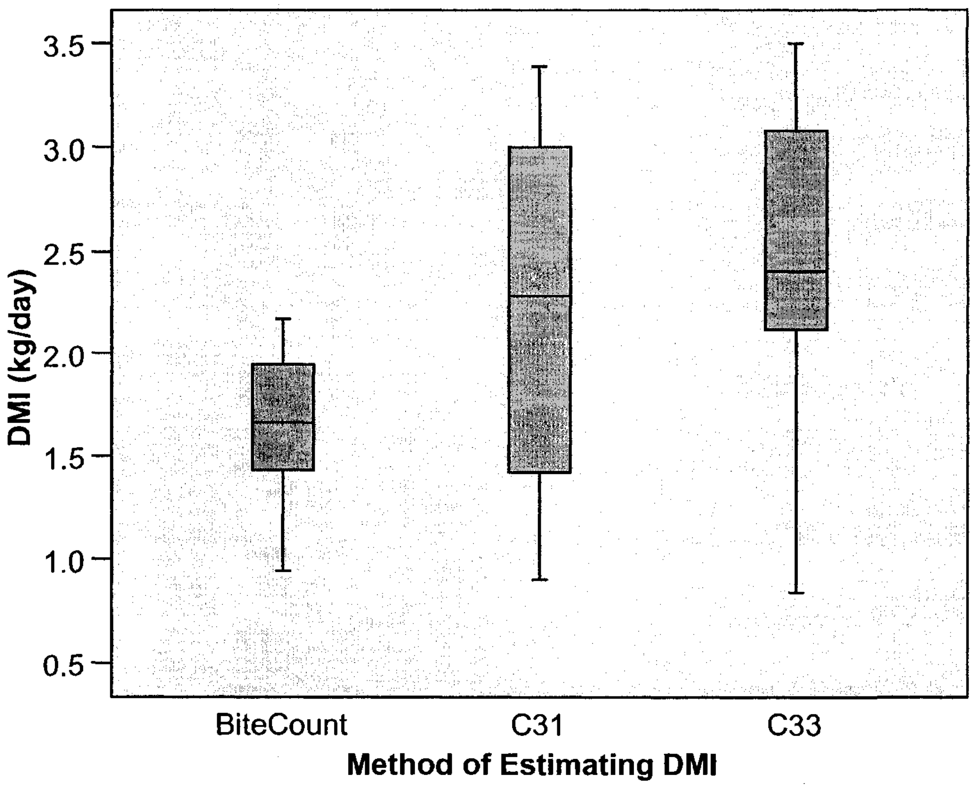

Figure 2.1. Comparison of DMI estimates for mule deer using the bite count, *n*-alkane C31 and *n*-alkane C33 methods during summer and fall of 2004/05.

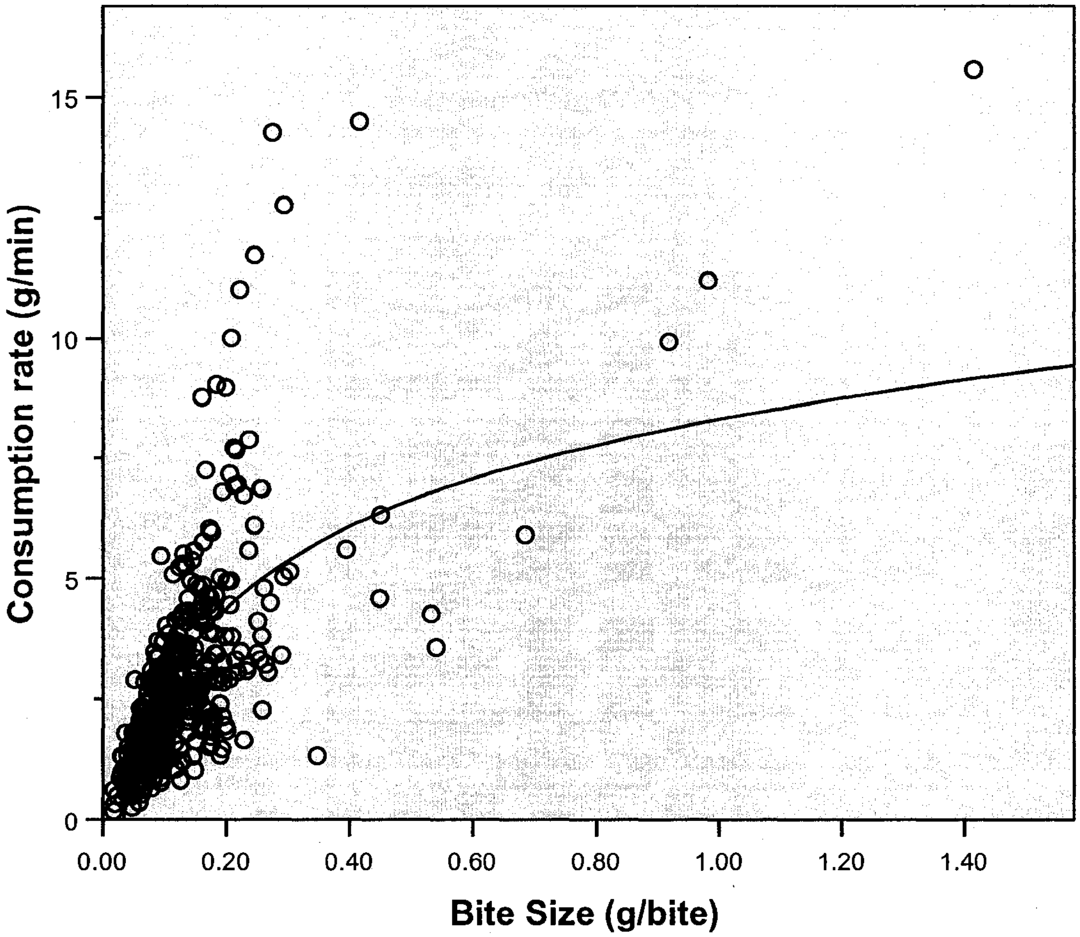

Figure 2-2. Consumption rates in relation to bite size for mule deer (Y = Ln 2.44x + 8.03; r^2 =0.47; $p<0.0001$).

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Chapter 3. Animal-Unit Equivalence of Bison, Wapiti and Mule Deer

3.1 Introduction

Animal-unit equivalence is used to quantify relationships among ungulates and their food supply and to estimate stocking combinations and densities (Stoddart and Smith 1955; Scarnecchia 1990; Holechek et al. 2004). Models have been developed to test assumptions of animal-unit equivalents in domestic livestock (Scarnecchia and Gaskins 1987) and several wild ungulates (Kinyua and Njoka 2001), yet few field studies provide estimates for free-ranging ungulates (Holechek et al. 2004), especially in multi-species systems. This is mostly because of difficulties obtaining accurate estimates of dry matter intake (Mayes and Dove 2000). Much ambiguity remains regarding the definition and utility of animal-unit equivalents (Scarnecchia 2004), and a lack of standardized terminology hampers effective management practices (Fleischner 1994). An acceptable calibration of animal-unit equivalents for ungulates is to determine forage intake in relation to body mass (Scarnecchia 2004).

The traditional standard animal-unit is one domestic cow weighing 454 kg (1000 lbs) with or without calf less than 6 months of age (Stoddart and Smith 1955). Animal-unit equivalents of other species have been given as 1.8 bison, 0.70 wapiti and 0.15 mule deer (Holechek 1988). Expressing forage intake (kg/day) as a percentage of body mass (%BM) is one method of standardization (Holechek et al. 2004). A basic assumption is that ungulates will consume the equivalent of 2-3% of their body mass per day, but it

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does not account for dietary differences or opportunities to express forage preferences on heterogeneous pastures (Hobbs and Carpenter 1986; Kinyua and Njoka 2001; Scarnecchia 2004).

Forage intake by ungulates can be expressed relative to metabolic mass (g/kg/day $BM^{0.75}$), which is derived from allometric scaling of inter-specific metabolic rates (Kleiber 1947). The ecological significance of this principle is that larger animals are more efficient at utilizing energy than smaller animals, as they have lower metabolic requirements per unit of body mass, but this may shift with quality of diet (Illius and Gordon 1991). The benefit of using metabolic mass rather than total body mass for determining animal-unit equivalents is that it standardizes interspecies comparisons based on metabolically active tissue. Alternatively, intake can be expressed relative to digestive capacity (kg) which scales closer to body mass ($BM^{1.0}$). For any herbivore guild, the challenge is to determine what is best for interspecies comparisons.

An essential component for quantifying animal-unit equivalence is a reliable technique to estimate dry matter intake. Previous techniques have relied on estimating percentage of pasture plant removal, measuring faecal output and digestibility, monitoring fistulated animals, or behavioural observation of foraging parameters (bite rate x bite size x foraging time) (Jiang and Hudson 1992). The use of inert markers to estimate forage intake has been challenging due to the requirement of daily dosing or the approximations associated with single-dose methods (Jiang and Hudson 1992; Rutley and Hudson 2000), but controlled release devices (CRDs) have opened opportunities for animals that cannot be repeatedly handled (Ellis et al. 1981). Odd-chain *n*-alkanes (C_{31}, C_{33}) found in plant cuticular wax have been used in combination with synthetic *n*-alkanes (C_{32}, C_{36}) released from the CRD to estimate forage intake and diet digestibility of grazing ruminants (Mayes et al. 1986). The *n*-alkane ratio technique has been used in single-species research with sheep and cattle (Mayes and Dove 2000), red deer (Heydon et al. 1993), wapiti (Gedir and Hudson 2000), fallow deer (Ru et al. 2002) and mule deer (Kuzyk and Hudson 2006), but not in bison, or in multi-species systems.

Our objective was to quantify animal-unit equivalence of three free-ranging ungulates on sympatric aspen parkland ranges using individual animal mass and dry matter intakes estimated with *n*-alkane markers. We evaluated dry matter intake for bison, wapiti and mule deer based on percent body mass and metabolic mass, and conducted detailed comparisons between bison and mule deer. We predicted dry matter intake would equate to 2-3% of body mass and dry matter intake expressed as percent body mass and metabolic mass would not differ among bison, wapiti, or mule deer. Diet digestibility was estimated to determine if forages consumed by each species compared favorably with other empirical values.

3.2 Materials and Methods

3.2.1 Study Area

This research was conducted at the University of Alberta Precision Ranching Facility in east-central Alberta (53 °N and 111° 31' W). This area is an aspen parkland habitat (Strong 1992) having a climate of long winters and short summers with mean temperatures of -12°C in December and 17°C in July. Predominant trees are trembling aspen and balsam poplar interspersed with grasslands and semi-permanent bodies of water. Understory vegetation contains rose, raspberry, Canadian gooseberry, serviceberry and snowberry. Grassland plants include rough fescue, smooth brome, bluegrass, blue grama, strawberry and asters. Willow, sedges, Canada thistle and dandelion occur in moist sites (Strong 1992).

3.2.2 Experimental Design and Animals

This research was part of a larger study examining the impact of ungulates on rangelands using mixed (bison, wapiti, mule deer) and tandem (successions of bison, wapiti, mule deer) assemblages of ungulates. Each assemblage was contained in a 3-7 ha fenced (2.4 m high) paddock with similar species of vegetation but in varying amounts (Didkowsky 2006). Bison, wapiti and mule deer were together in mixed paddocks for 45 days, which differed from tandem paddocks where each of the three species was rotated through the same paddock on 15 day intervals (45 day total). The 45-day trials consisted of nine paddocks: three mixed, three tandem lead by bison, wapiti, mule deer, and three tandem lead by mule deer, wapiti, bison. In 2004, mixed paddocks contained two bison, two wapiti, and two mule deer while tandem paddocks each contained four bison, four wapiti and four mule deer. Stocking rates were adjusted in 2005 to conform with objectives of the larger study with mixed paddocks having three bison, three wapiti, and two mule deer, while tandem paddocks each had six bison, three wapiti and three mule deer. These stocking rates, expressed as animal-unit-months (AUM), equated to 1.2-2.0 AUM/ha in 2004 and 1.7-2.8 AUM/ha in 2005. Grazing impacts were considered light to moderate as the trials lasted 90 days of a 120-day growing season and the study area was not grazed the year prior (2003) to the experiment.

Our experimental units were individual animals dosed with *n*-alkane capsules in separate paddocks. All our trials were 15 days long to correspond with finite release rates of *n*-alkane capsules (maximum 20 days, Captec ©™) and tandem rotations (15 days). There were 4 resulting trials: 1-15 September 2004 and the first 15 days of June, July and September in 2005. One trial was conducted with all three species (September 2004) and three other trials (June 2005, July 2005, September 2005) compared dry matter intake and diet digestibility between bison and mule deer. The July 2005 trial was the only one where bison or mule deer were not the initial ungulate in the tandem paddocks. During that trial, bison followed mule deer and wapiti, whereas mule deer followed bison and wapiti. During the July 2005 trial, only bison and mule deer in tandem paddocks were dosed with *n*-alkane capsules. During this time, intra-specific comparisons of bison and mule deer in mixed versus tandem paddocks could not be conducted concurrently because ungulates in mixed paddocks could not be dosed with *n*-alkane capsules 30 days into a 45-day trial, as it would disturb the animals and compromise the larger study.

The experimental animals included 12 bison [1.8 ± 0.6 years (mean ± SD); 408.2 ± 52.5 kg (mean ± SD)], 3 wapiti (7.7 ± 0.6 years; 314.7 ± 16.2 kg) and 11 mule deer (4.8 ± 2.1 years; 60.1 ± 5.8 kg). All were adult non-lactating females with the exception of two bison, which had calves at heel during the September 2005 trial. Ungulates were individually weighed at the beginning and end of each trial. All mass measurements were standardized using those taken at the beginning of each mixed trial (1 June 2005, 1 September 2004, 1 September 2005) because in July 2005 no animals in mixed paddocks were given *n*-alkane capsules. Mean metabolic mass was 90.7 $kg^{0.75}$, 74.7 $kg^{0.75}$, 21.6 $kg^{0.75}$ for bison, wapiti and mule deer, respectively (Table 3-1). All experimental animals were marked with ear tags for individual identification and some were instrumented with radiocollars (Telonics TGW-3570, GPS/VHF) as part of the larger study. Radiocollars were utilized for rapid location of dosed animals. All animal handling was conducted through the University of Alberta and approved by the Faculty Animal Policy and Welfare Committee (Protocol HUDS 2004–33B), subject to guidelines of the Canadian Council on Animal Care.

3.2.3 *n*-Alkane Capsules and Calculations

At the commencement of each trial, experimental animals were given one *n*-alkane capsule and placed in separate paddocks. We administered 21 capsules to 12 bison, 3 capsules to 3 wapiti, and 23 capsules to 11 mule deer. Individual bison and mule deer received between 1 and 5 capsules during the experiment. Large *n*-alkane capsules designed for cattle (100-300 kg; Captec ©™) were administered orally with a dosing-gun (Captec ©™) into the rumen of bison and wapiti. Small *n*-alkane capsules designed for domestic sheep (25-80 kg; Captec ©™) were administered to mule deer. Large capsules had a specified release rate of 200 mg/day for C_{32} and C_{36}, whereas the small capsules had release rates of 50 mg/day for C_{32} and C_{36}. Release rates were considered stable for 20 days. Previous experiments using small capsules found release rates of 41.7 mg/day for C_{32} in domestic sheep (Dove et al. 1991), and 40 mg/day for C_{32} and 37 mg/day for C_{36} in fallow deer (Ru et al. 2002). Possible differences in release rates could be due to dissimilar rumen function among species (Ru et al. 2002) and therefore, our calculations of dry matter intake and diet digestibility for mule deer followed the protocol for fallow deer (Ru et al. 2002).

Concentrations of even-chained *n*-alkanes (C_{32}, C_{36}) were determined from fresh faeces collected 7-10 days after commencement of the trial, which was the manufacture's (Captec ©™) specified time for synthetic *n*-alkanes to achieve steady state. Experimental animals were followed until 1-4 samples (10-20 g) of fresh faeces were collected for individual analysis. Faecal samples were handled with rubber gloves, put in plastic bags and placed in a deep freeze within 6 h of collection. Samples of odd-chained *n*-alkanes (C_{31}) were gathered from vegetation samples using the simulated bite technique, which entails an observer following a focal animal and collecting the plants and plant parts consumed by the ungulate (Hudson and Watkins 1986). The vegetation samples were hand-plucked and meant to represent bite sizes of bison (Hudson and Frank 1987), wapiti (Hudson and Watkins 1986) and mule deer (Kuzyk and Hudson 2006). A key assumption for this method is that the bison, wapiti and four mule deer were habituated to people, enabling observers to approach within 1-30 m without altering the foraging behaviour of the animals. The other seven mule deer could not be approached to gather vegetation samples. Therefore, because of a lack of tame animals and other logistical constraints, vegetation samples were collected from adjacent paddocks (e.g., vegetation samples from tame deer in mixed paddocks were used for non-tame deer in mixed paddocks). Vegetation samples (18-197 g) were oven-dried at 60°C for 48 h.

All *n*-alkane concentrations (C_{31}, C_{32}, C_{36}) were determined at the Department of Animal Science, University of Manitoba, following Boadi et al. (2002) and Moshtaghi Nia and Wittenberg (2002). Modifications to these methods included a gas chromatograph (Varian 3900) with a fused capillary column (30m x 0.32cm x 0.25 *u*m film) that ran for 18 min using He as the carrier gas. Dry matter intake (DMI) was calculated by pairing C_{32} with C_{31} following Gedir and Hudson (2000):

$$\text{DMI (kg/day)} = (D_{32} \text{ x } Fn/F_{32}) / [Hn - (Fn/ F_{32}) \text{ x } H_{32}]$$

where D_{32} is the release rate of synthetic C_{32} (mg/day) and F_{32} and H_{32} are concentrations (mg/kg DM) of C_{32} recovered from faecal samples and vegetation, respectively. Fn and Hn represent the respective concentrations (mg/kg DM) of natural odd-chained alkanes (C_{31}) in faeces and vegetation.

Percent diet digestibility was calculated following Heydon et al. (1993):

$$\text{Digestibility} = \frac{1 - (0.96 \text{ x } D_{36})/ F_{36}}{\text{DMI}}$$

where 0.96 is a correction factor for partial digestibility of C_{36}, D_{36} is the release rate of dosed C_{36} (mg/day) and F_{36} is the concentration (mg/kg DM) of C_{36} from the recovered faeces.

3.2.4 Statistical Analysis

Non-parametric tests were applied (SYSTAT Version 11.0; SPSS Version 14.0) because of the small number of experimental animals (Zar 1999). A Kruskal-Wallis test compared dry matter intake and diet digestibility among bison, wapiti and mule deer. A Mann-Whitney *U*-test was used to compare dry matter intake and diet digestibility between bison and mule deer. The trial in July 2005 consisted of three bison and three mule deer in tandem paddocks, which was inadequate for an independent statistical test, so these data were pooled for comparisons between bison and mule deer, and intra-specific comparisons. Intra-specific comparisons of bison and mule deer in tandem versus in mixed paddocks were evaluated with a Mann-Whitney *U*-test. Data for intra-specific comparisons were pooled (September 2004, June 2005, September 2005), but the data did not include July 2005 as no animals in mixed paddocks had *n*-alkane capsules during that time. Values with $P < 0.10$ were considered significant because of the limited number of experimental animals.

3.3 Results

No synthetic *n*-alkane was found in 2 of 21 bison faecal samples (1 September 2004 and 1 September 2005) and 3 of 23 mule deer faecal samples (1 September 2004, 1 June 2005, and 1 September 2005), so the *n*-alkane capsules were presumed to have been regurgitated. Comparisons among bison, wapiti, and mule deer were limited to one trial (September 2004) where animal-unit equivalents were determined for body mass and metabolic mass (Table 3-1). Dry matter intake differed among three species when calculated as kg/day (Kruskal-Wallis test, $p = 0.009$) and percent body mass (Kruskal-Wallis test, $p = 0.014$), but not as metabolic mass (Kruskal-Wallis test, $p = 0.24$). Digestibility of diets did not differ among species during this trial (Kruskal-Wallis test, $p = 0.15$) (Table 3-2).

During the September 2005 trial, the two bison with calves consumed 8.4 kg/day and 6.6 kg/day, respectively, which was near the mean of 7.0 ± 0.6 kg/day (±SE), and less than 2% of body mass (1.9 % BM, 1.5 % BM). Absolute intake (kg/day) by bison was greater than that of mule deer in all time-period comparisons (Tables 3-2, 3-3), and when pooled with the July 2005 data (Mann-Whitney *U* test, $p < 0.0001$). In contrast, when expressed as percent body mass, mule deer had greater intakes than bison in September 2004 (Mann-Whitney *U* test, $p = 0.016$) and September 2005 (Mann-Whitney

U test, $p = 0.006$), but not during June 2005 (Mann-Whitney *U* test, $p = 0.273$). Using pooled data (all four time periods), intake expressed as percent body mass differed between bison and mule deer (Mann-Whitney *U* test, $p = 0.007$). No difference was detected in dry matter intake between bison and mule deer expressed as metabolic mass during September 2004 (Mann-Whitney *U* test, $p = 0.754$), June 2005 (Mann-Whitney *U* test, $p = 0.584$), September 2005 (Mann-Whitney *U* test, $p = 0.201$) (Tables 3-2, 3-3), or when pooled with the July 2005 data (Mann-Whitney *U* test, $p = 0.530$). Digestibility of diets differed between mule deer and bison in all time period comparisons (Tables 3-2, 3-3) and when pooled with the July 2005 data (Mann-Whitney *U* test, $p = 0.001$).

Intra-specific comparisons of dry matter intake and diet digestibility were analyzed for bison and mule deer in mixed versus tandem paddocks. No difference was found for either bison or mule deer in dry matter intake expressed as absolute amounts (bison: Mann-Whitney *U* test, $p = 0.791$; mule deer: Mann-Whitney *U* test, $p = 0.159$) or metabolic mass (bison: Mann-Whitney *U* test, $p = 0.958$; mule deer: Mann-Whitney *U* test, $p = 0.104$). Intake expressed as percent body mass did not differ among bison (Mann-Whitney *U* test, $p = 0.958$), but was marginally greater for mule deer in tandem versus mixed paddocks (Mann-Whitney *U* test, $p = 0.082$). Digestibility of diets selected by mule deer or bison did not differ for either species between tandem and mixed paddocks (bison: Mann-Whitney *U* test, $p = 0.791$; mule deer: Mann-Whitney *U* test, $p = 0.233$).

3.4 Discussion

We derived animal-unit equivalencies of free-ranging sympatric bison, wapiti and mule deer using individual body mass measurements and dry matter intake determined by *n*-alkane markers. Previous suggestions to refine animal-unit equivalents were based on incorporating dietary differences among species. Hobbs and Carpenter (1986) disputed Scarnecchia's (1985) contention that animal-unit equivalents for sympatric ungulates should not be weighted to include dietary overlap. Although numerous studies document diets of sympatric ungulates (Hobbs and Carpenter 1986), animal-units are based on intake and more studies with known animal mass and intakes are required.

When refining animal-unit equivalence for bison, wapiti, and mule deer, we found that dry matter intake differed among species in absolute terms, but significance was variable when expressed as percent body mass. Total intake differences among species are expected owing to the wide contrast of body sizes and diverse anatomical and physiological features (Illius and Gordon 1991; Robbins et al. 1995; Clauss et al. 2003). Values of total forage intake from our study concur with other research on bison (Rutley and Hudson 2000), wapiti (Collins and Urness 1983; Gedir and Hudson 2000) and mule deer (Alldredge et al. 1974; Wickstrom et al. 1984), but comparable studies on intake of these species grazing sympatrically are not available. Foraging relationships among sympatric bison, wapiti and mule deer are rarely studied (Singer and Norland 1994) mostly because of the limited range of bison. In Yellowstone National Park, niche and habitat overlaps were minimal among bison, wapiti, and mule deer mostly because of differences in dietary preferences (Singer and Norland 1994).

Holechek et al. (2004) suggested that the preferred estimate of daily dry matter intake for ungulates is 2% of body mass. Our values ranged from 2-4% for bison, wapiti and mule deer, and are in general agreement (Holechek et al. 2004), but species differences emerged. Intakes of dry matter by bison were generally less than the 2% body mass, whereas mule deer had intakes that often ranged closer to 4% of body mass. We found dry matter intake expressed as percent body mass differed among sympatric bison, wapiti and mule deer, between bison and mule deer in 3 of 4 comparisons, and was greater for mule deer in tandem versus mixed paddocks. In June 2005 intake expressed as percent body mass did not differ between bison (2.5 %BM) and mule deer (3.6 %BM), which may have been due to the high consumption of vegetation during the spring flush. One problem with using body mass in comparative studies is that different mass measurements can be used for the same species (Miller 2000), as is the case with bison in our study. Mean body mass of bison used by Holechek (1988) to calculate animal-units was 818 kg, whereas our bison weighed 408 kg, and were primarily young-aged animals (1.8 ± 0.6 years). More refined comparisons of animal-units could be achieved by using age and gender-specific mass along with herd composition.

Allometric scaling has been applied to African ungulates (Bell 1971; Jarman 1974) and is widely known as the Jarman-Bell Principle (Geist 1974). Because relative metabolic rate decreases with increasing body size, but digestive capacity stays at a constant portion of body mass, larger animals should be able to subsist on a diet of lower quality than smaller ones (Demment and VanSoest 1985; Illius and Gordon 1991; Clauss and Hummel 2005). This was found in my study where digestible dry matter intake ranged between bison (32.5 g/kg/d) and mule deer (84.9 g/kg/d) during fall. The small sample size of experimental animals precluded us from using an isometric scalar to examine this approach, but mule deer in this study weighed an average of 60 kg and bison weighed an average of 408 kg, a 6.8-fold difference in body size, yet there was no significant difference in intake based on metabolic mass.

Comparative foraging parameters of sympatric bison and mule deer have received some attention, with no evidence suggesting forage competition between these two species (Shaw and Meagher 2000). We found that bison and mule deer on sympatric ranges do not have equivalent intake based on percent body mass, but do in terms of metabolic mass. There was no difference in dry matter intake expressed as metabolic mass between bison or mule deer in tandem versus mixed paddocks, but a small sample size precluded reliable conclusions. In addition, bison are highly gregarious (Hudson and Frank 1987) and have limited interactions with wapiti (Miller 2000) or mule deer (Shaw and Meagher 2000). This may suggest that intra-specific interactions are as important as inter-specific interactions when evaluating dry matter intake related to functional interactions of ungulates (Kuzyk and Hudson 2006).

Digestibility of diets for ungulates is usually derived from *in vivo* or *in vitro* techniques, which may not provide accurate results (Spalinger 2000). We used an *n*-alkane marker (C_{36}) to determine diet digestibility of free-ranging animals and found values for bison (44% - 66%) to be similar to results using *in vitro* digestibility for bison using grasses (41- 67%) (Plumb and Dodd 1993) and sedges (60 - 70%) (Bergman et al. 2001), or bison fed alfalfa pellets (53%) (Galbraith et al. 1998). Our digestibility estimates for elk (68%) were similar to those for elk on compounded feeds (63%) (Gedir and Hudson 2000) and *in vitro* digestibility trials using grass hay (62%) (Baker and Hansen 1985), but lower than elk on pastures in May (85%) (Jiang and Hudson 1992). Mule deer in our study had diet digestibility values of 67% - 81% which is higher than ~45% digestibility of mule deer in pen trials (Baker and Hobbs 1987), *in vitro* digestibility trials using grass hay (58%, Baker and Hansen 1985) or white-tailed deer (*O. virginianus*) fed alfalfa pellets (49%, Galbraith et al. 1998).

3.5 Conclusion

The double *n*-alkane ratio technique is a practical technique for estimating dry matter intake and diet digestibility of free-ranging sympatric ungulates. It allowed us to test hypotheses specific to intake and produced measures that offer refinement of ungulate stocking rate calculations. We used experimental animals that were fed balanced rations during the winter, and were not lactating during the experiment, which provided good controls to examine intake among species. We provide evidence that intake based on percent body mass may not be uniform among sympatric ungulates in heterogeneous habitats. The majority of grazing systems support multiple species, yet most published values of dry matter intake are from single-species studies, and are expressed as percent body mass (Holechek et al. 2004: 331-332). Our values for animal-unit equivalents expressed as metabolic mass differ from those based on body mass (Holechek 1988; Holechek et al. 2004). Our result for mule deer calculated as metabolic mass (60 $kg^{0.75}$ = 0.22 animal-units) is 41% higher than using body mass (60 kg = 0.13 animal-units) and is 32% above the recommended stocking rate for mule deer derived from body mass (68 kg = 0.15 animal-units) (Holechek 1988; Holechek et al. 2004). This suggests smaller ungulates such as mule deer could potentially have a 30-40% greater impact on range use than previously thought and stocking rates should be adjusted according to metabolic mass. In addition, mule deer prefer foraging on highly nutritious plants and could affect the range by removing large quantities of such plants. Further elaborations of animal-unit equivalence should be directed to additional field-testing of multi-species systems and developing models of ungulate stocking rates using metabolic mass.

Table 3-1. Animal-unit equivalents (AU) expressed as mean body mass and mean metabolic mass of free-ranging bison, wapiti, and mule deer in an aspen parkland habitat in east-central Alberta during September 2004.

	Body Mass (kg)	Metabolic Mass ($kg^{0.75}$)	AU (kg)	AU ($kg^{0.75}$)
Bison (*n* = 12)	408.2	90.7	0.90	0.92
Wapiti (*n* = 3)	314.7	74.7	0.69	0.76
Mule deer (*n* = 11)	60.1	21.6	0.13	0.22

Table 3-2. Dry matter intake (DMI) and diet digestibility of bison, wapiti, and mule deer estimated with *n*-alkane markers in an aspen parkland habitat at the University of Alberta Ranch during 1-15 September 2004.

	Bison ($n = 5$)	Wapiti ($n = 3$)	Mule Deer ($n = 5$)	P
DMI (kg/day)	11.0±2.5 ^{a}	6.9±1.5 ^{ab}	2.7±0.2^{b}	**0.008**
DMI (%BM)	2.5±0.5 ^{a}	2.2±0. 5 ^{a}	4.4±0.3 ^{b}	**0.014**
DMI (g/kg/day BM$^{0.75}$)	114.8± 22.5	92.3±19.1	124.0±8.2	0.24
Digestibility (%)	59.6±12.0	67.6±9.3	78.0±2.8	0.15

Values are means ±1 SE. Within a row, means with the same letter do not differ at $p < 0.10$.

Table 3-3. A comparison of dry matter intake (DMI) and diet digestibility of bison and mule deer on summer and fall pastures in an aspen parkland habitat at the University of Alberta Ranch.

	1-15 June 2005			1-15 September 2005		
	Bison ($n = 6$)	Mule deer ($n = 5$)	P	Bison ($n = 5$)	Mule deer ($n = 6$)	P
DMI (kg/day)	9.5±1.3	2.1±0.5	0.006	7.0±0.6	2.5±0.3	0.006
DMI (%BM)	2.5±0.3	3.6±0.8	0.273	1.6±0.1	4.0±0.6	0.006
DMI (g/kg/day $BM^{0.75}$)	110.9±14.7	99.6±22	0.584	73.1±6.5	112.0±16.3	0.201
Digestibility (%)	65.9±3.8	81.1±3.9	0.028	44.4±6.2	75.8±3.0	0.006

Note: Values are means ± 1 SE.

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Chapter 4. Estimating Carrying Capacity for an Ungulate Guild

4.1 Introduction

Determining the number of animals that a land base can sustain presents a persistent challenge particularly in multi-species grazing systems (Leopold 1933; Stoddart and Smith 1955; Beck et al. 2006; Dimond and Armstrong 2007; Metzger et al. 2007; Morellet et al. 2007). This sustained stocking rate is commonly known as carrying capacity (Caughley 1979; Miller and Wentworth 2000) which can be used as a measure to balance ecological, economic, and aesthetic concerns that face resource managers (Bai et al. 2001; Angassa and Oba 2007; Cabezas and Moreno 2007; Tepedino et al. 2008).

In practice, carrying capacity is rarely measured (Morris and Mukherjee 2007) and initial estimates are progressively adjusted in adaptive management programs. Also, the term "carrying capacity" is used in numerous ways, adding to the complexity of the problem (McNab 1985; Caughley 1979). Ecological carrying capacity (K) is usually defined as the maximum number of animals a defined area can support in relation to the available resources (McCullough 1992), where K is primarily limited by forage (Caughley 1979; Miller and Wentworth 2000). Population biologists define ecological K as an equilibrium at which population growth rate equals zero (Caughley 1979; Varley and Boyce 2006). This differs from economic K, which prescribes a measure of herbivores with available vegetation (Caughley 1979), where limits such as ungulate densities to achieve a pre-determined removal of available forage are assigned to the system (Stoddart and Smith 1955; Stewart et al. 2006). Range managers use economic K to maximize stocking rates without degrading forage quantity or quality or altering plant community succession in undesirable ways (Caughley 1979; Vetter 2005).

Calculations specific to forage use by ungulates make use of plant removal rates and safe-use factors (SUF) where forage removal by native ungulates is commonly set between 35-50% of annual growth to allow for variation in forage availability (Wallmo et al. 1977; Harlow 1984; Irby et al. 2002). The forage reserve (i.e., the proportion of the forage remaining) is often used to provide a buffer against stochastic environmental conditions and prevent degradation of vegetation during years with unfavorable growing conditions (Willoughby et al. 2006). Another hedge provided by the forage reserve is to provide sufficient opportunity for diet selection to meet seasonal quality thresholds. Although range scientists and managers frequently use various vegetative measures of range condition to ensure long-term sustainability (Holechek et al. 2004; Stephenson et al. 2006), criteria for evaluating appropriate stocking levels seldom include measures related to the animals present in the system (McLeod 1997; Focardi and Tinelli 2005; Traill and Bigalke 2007).

Reliable estimates of the daily dry matter intake by ungulates are considered central to assessing carrying capacity and determining animal unit equivalents (Holechek 2004; Willisch and Ingold 2007; Owen-Smith and Mills 2008). In a multi-species system, dry matter intake varies among species, but can be generalized in terms of their digestive capacity and body size (Van Soest 1994). Large ungulates are generally bulk feeders that consume large amounts of low quality grass (Codron et al. 2007), whereas smaller ungulates are concentrate selectors and consume smaller amounts of highly digestible forage such as forbs or browse (Wiegmann and Waller 2006; Zimmerman et al. 2006). Medium-sized ungulates are often intermediate feeders and consume varying proportions of shrubs and grass (Torstenson et al. 2006).

Forage demand can be measured as the amount of forage consumed per day and is often standardized as animal-units (Stoddart and Smith 1955). One animal-unit is usually considered to be the body mass equivalent of one domestic cow either with a calf less than 6 months old (454 kg) or without a calf. One animal unit is assumed to require 26 kg of forage (based on air-dried weight) per day (Stoddart and Smith 1955; Holechek et al. 2004). One animal-unit month is defined as the sum of the daily requirements accumulated over one month or approximately 780 kg of forage (Society of Range Management 2004). Perhaps because of its simplicity, the animal-unit concept has been widely adopted by range managers concerned with grazing livestock that are either similar in dietary preferences or graze pastures with little opportunity for selection (Stoddart and Smith 1955; Kazmaier et al. 2001; Dong et al. 2007; Patton et al. 2007). However, there are difficulties extending the animal-unit concept to wild ungulates (Holechek et al. 2004; Kuzyk and Hudson 2007).

In contrast to seasonal livestock grazing, requirements for wild ungulates require forage to be characterized at the scale of an "animal-unit-year" as they remain present on the landscape over a full twelve month period without supplementation. Furthermore, despite assigning a value of anticipated forage removal for each ungulate species (Holechek et al. 2004), forage specialization of wild ungulates and seasonal shifts in diet (Spalton 1999; Owen-Smith 2002; Hernandez and Laundre 2005) preclude forage use estimates at the scale of the animal-unit month. As such, monthly or seasonal diets and intakes of wild ungulates must be summed to annual totals. Lastly, despite the fact that most wild ungulates co-exist in multi-species systems (Wallis De Vries 1995; Wegge et al. 2006; Jenkins et al. 2007; Yoshihara et al. 2008), there is limited information associated with concurrent daily intakes of multiple species (Holechek et al. 2004; Kuzyk and Hudson 2007).

Elk Island National Park (EINP) is a small, enclosed and carefully monitored park (194 km^2) in western Canada that provides an ideal opportunity to explore the concept of economic carrying capacity. The park supports four species of ungulates and is a relatively controlled environment due to the lack of predators and complete enclosure of the park by a 2.1-m page wire fence. Because of the lack of predators and the presence of the fence, each year resource managers are forced to manage ungulate numbers relative to the available vegetation. The fence contains plains bison, wood bison and wapiti, but allows movement of moose, white-tailed deer and mule deer (Blyth 1995). The ungulate guild within the park approaches the biomass and productivity of multi-species grazing systems of East Africa (Telfer and Scotter 1975). Because there is a high density of ungulates (11/km^2) in a small area, and the movements of ungulates are relatively fine-scale and thus may be sustained by resource partitioning (Cairns and Telfer 1980), carrying capacity can be examined through a forage allocation approach.

Linear programming is generally used to determine an optimal combination given a set of decision variables that are subject to a one or more constraints, and has been used routinely for solving resource allocation problems (Glover and Conner 1988; Forchhammer and Boomsma 1995; Buongiorno and Gilless 2003). Others have used linear programming in range management (Van Dyne 1966; Hudson and Blyth 1986; Irby et al. 2002) as well as for other wildlife and plant-related questions with varying degrees of success. For example, Hastings et al. (2006) used linear programming to determine the optimal age or stage class to control invasive plant species under the constraints of time and financial budget. Belovsky (1978) used linear programming to examine optimal summer diet of moose, which consisted of a combination of aquatic and terrestrial plants. Because plants vary in nutrient quality, it was assumed that a varied diet selection was required to produce an optimal diet of energy-rich but sodium-poor terrestrial plants, combined with energy-poor and sodium-rich aquatic plants. Belovsky (1978) determined optimal diet was constrained by 1) energy, 2) sodium content, and 3) rumen size. Hobbs (1990) later contested Belovsky's approach with specific criticisms of digestive constraints and questioned the high success of predictability. Although Belovsky's formulation has been criticized as inappropriate for testing the optimal foraging theory (Belovsky 1978; Hobbs 1990), this is not an indictment of linear programming as a method that has been used successfully to examine forage allocation across a guild of ungulates. Irby et al. (2002) used linear programming to find solutions for the optimal allocation of available forage to multiple ungulates in Theodore Roosevelt National Park, North Dakota.

The objective of this chapter was to develop an approach and a template for the annual estimate of carrying capacity for bison, moose, wapiti, and deer in the Main Park (134 km^2) of EINP (Figure 4-1). I used linear programming to calculate optimal solutions for the maximum number and the maximum biomass of ungulates given pre-set management constraints (sustainable use of park vegetation and minimum viable populations of bison and wapiti). I used an animal-unit-year approach by matching annual forage supply (kg/ha of grass, forbs, shrubs across four primary habitats) (Table 4-1) with the corresponding ungulate demand estimated from seasonal diets and intakes summed annually (kg forage per ungulate per year) (Table 4–2). Feasible solutions require that resources last for one full year, so solutions with seasonal shortfalls are slated. This approach applies the principle of carrying capacity to evaluate an application for resource management and is not validated against forage utilization estimates.

Linear programming as applied here requires that the proportion of total forage used annually be set as one of the initial input variables. Therefore, given any proportion of total annual forage used, an estimate of the annual forage supply, an estimate of the total ungulate demand, and an appropriate model structure, the optimal combination of bison, moose, wapiti and deer in biomass, abundance or other measure of value can be calculated. Finally, I used known densities of ungulates in the park (December 2006) and matched these densities to the optimal stocking solutions reported at each level (total annual forage used) tested. These solutions can be viewed as initial estimates of economic carrying capacity for the ungulate guild and provide novel insights and a starting point for determining carrying capacity and management strategies for the park.

4.2 Material and Methods

4.2.1 Study Area

I used the Main Park (hereafter – park) of EINP in order to allow for a comparison between the work conducted here and that of Telfer and Scotter (1975). EINP is located in the Beaver Hills approximately 40 km east of Edmonton, Alberta, Canada (53° 36' N and 112° 51' W) (Figure 4-2). The park is part of the Cooking Lake moraine at elevations 30-60 m above surrounding areas and has several shallow lakes. The park is surrounded mostly by agricultural land and has a four-lane highway (Highway 16) bisecting the park into the Main Park on the north side (134 km^2) and the Wood Bison Isolation Area (60 km^2) on the south side. The climate is characterized by cold winters and warm summers with mean temperatures of -14°C in December and 16°C in July. Annual rainfall precipitation is 496 mm, of which 375 mm falls as rain and 121 mm as snow (Environment Canada 2006).

Moose, wapiti, white-tailed deer and mule deer occur throughout the park, but plains bison are restricted to the Main Park and wood bison to the Isolation Area. In December 2006, 476 plains bison, 72 moose, 333 wapiti and 78 deer inhabited the Main Park (Cool 2006). Minimum viable populations (MVP) are maintained at pre-calving populations of 175 bison and 350 wapiti (Wilson and Zitlau 2003). Historically, wolves, grizzly bears (*Ursus arctos*), and black bears (*Ursus americanus*) occupied the area, but today coyotes (*Canis latrans*) and lynx (*Lynx canadensis*) are the largest predators, with cougars (*Felis concolor*) (Hood and Neufeld 2004) and black bears occasionally recorded. Beaver (*Castor canadensis*) are abundant and influence water levels and plant succession adjacent to wetlands (Hood et al. 2007).

EINP exists in a transitional zone between the prairie and boreal forest with vegetation classified as dry mixedwood boreal forest (Willoughby et al. 2006). Trembling aspen is the dominant tree species and commonly co-exists with balsam poplar or white birch (*Betula papyrifera*), with additional small areas of white spruce (*Picea glauca*) and black spruce (*Picea mariana*) in the northern part of the park. Shrub understories consist of beaked hazel (*Corylus cornuta*), dogwood (*Cornus stolonifera*), chokecherry (*Prunus virginiana*), willow, prickly rose (*R. acicularis*), raspberry and other shrubs. Common native grasses are *Agropyron* spp., *Elymus innovatus* and *Oryzopsis asperifolia*, with introduced species being *Trifolium* spp., *Bromus* spp. and *Poa* spp., whereas wet meadows are dominated by *Calamagrostis canadensis* and hydric *Carex* spp. often with an overstory of *Salix* spp. (Byth and Hudson 1987). Vegetation composition is further described by Bork et al. (1997a, b) and Hood et al. (2007).

4.2.2 Linear Programming

Although the linear programming framework is deterministic, it can be used to solve complex resource allocation problems such as allocating a limited forage supply to a guild of ungulate species. I used the Microsoft Exel© linear programming "Add-In" (i.e., Microsoft Excel Solver ©). The objective function dictated how the ungulate guild (i.e., bison, moose, wapiti, deer) could be optimized to acheive 1) maximum number of individuals (animals/ha) and 2) maximum biomass (kg/ha) under the constraints of forage availability and minimum viable populations for species where this is a concern (i.e., bison and wapiti) (Figure 4-1).

The two main assumptions in linear programming are (1) the objective function (Z) is linear and is of the form $Z = (x_1 + x_2 + x_3 + x_4)$ and (2) all variables are no non-negative (e.g., densities) or more formally, all $x_1, x_2, x_3, x_4 \geq 0$.

Thus, for maximum number of individuals (animals/ha):

$$Z = c\,(x_1 + x_2 + x_3 + x_4)$$

Where:

Z = objective function

c = area of park (13,400 ha)

x_1= bison density, x_2 = moose density, x_3 = wapiti density, x_4 = deer density

For maximum biomass (kg/ha):

$$Z = c_1x_1 + c_2x_2 + c_3x_3 + c_4x_4$$

Where:

Z = objective function

c_1= biomass/bison, c_2= biomass/moose, c_3= biomass/wapiti, c_4= biomass/deer

x_1= bison density, x_2 = moose density, x_3 = wapiti density, x_4 = deer density

Subject to constraints of annual availability of grass (b_1), forbs (b_2) and shrubs (b_3):

$$a_{11}x_1 + a_{12}x_2 + a_{13}x_3 + a_{14}x_4 \leq b_1$$

$$a_{21}x_1 + a_{22}x_2 + a_{23}x_3 + a_{24}x_4 \leq b_2$$

$$a_{31}x_1 + a_{32}x_2 + a_{33}x_3 + a_{34}x_4 \leq b_3$$

Where total species-specific forage intake can be characterized in the following form:

For grass:

$a_{11}x_1$ = annual grass requirements per bison

$a_{12}x_2$ = annual grass requirements per moose

$a_{13}x_3$ = annual grass requirements per wapiti

$a_{14}x_4$ = annual grass requirements per deer

b_1 = annual availability of grass

And for forbs:

$a_{21}x_1$ = annual forb requirements per bison

$a_{22}x_2$ = annual forb requirements per moose

$a_{23}x_3$ = annual forb requirements per wapiti

$a_{24}x_4$ = annual forb requirements per deer

b_2 = annual availability of forbs

And for shrubs:

$a_{31}x_1$ = annual shrub requirements per bison

$a_{32}x_2$ = annual shrub requirements per moose

$a_{33}x_3$ = annual shrub requirements per wapiti

$a_{34}x_4$ = annual shrub requirements per deer

b_3 = annual availability of shrubs

In addition, I added genetic constraints to ensure minimum viable populations for bison (x_1) and wapiti (x_3) where:

$x_1 \geq 0.02$ animals/ha

$x_3 \geq 0.03$ animals/ha

4.2.3 Forage Supply by Habitats

Forage supply was estimated using annual production of three forage classes (grass, forbs, shrubs) across four habitat types, and subsequently matched with the annual dietary preferences and forage intake levels of each ungulate species (Van Dyne 1966; Hudson and Blyth 1986; Irby et al. 2002). A forage "production by habitat" availability matrix summarized forage biomass within each of the four major habitat types of EINP

(Table 4-1). A Geographic Information System was used to calculate the area of each habitat type based on the 1995 Alberta Vegetation Inventory coverage with refinements made using expert knowledge of the park (N. Cool, Parks Canada, Environmental Resource Conservation, personal observation) to adjust for current differences in wetland coverage (Table 4-1). EINP does not have a complete data set of grass, forb and shrub forage biomass (kg/ha) for each of the four predominant habitats. Consequently, I used published sources from EINP for grass biomass for two habitat categories (Bork et al. 2001), an unpublished data set from EINP for grass, forb and shrub values for aspen habitats (Best and Bork 2004), with the remaining values taken from data compiled across the dry and central mixedwood subregions of Alberta (Alberta Sustainable Resource Development 2004; Willoughby et al. 2006) (Table 4-1).

4.2.4 Forage Needs of Ungulates

For each ungulate species, forage intake (kg/d) and % forage class in the diet from the four seasons were summed to annual totals (Table 4-2). Data on seasonal diet proportions for all species and seasons specific to EINP were used (Holsworth 1960; Cairns 1976; Renecker 1987b; Cool 1992) with the exception of the fall diet of bison (P. Dewitt, unpublished data), summer and fall diets of moose (Renecker 1987a) and mule deer (P. Dewitt, unpublished data), which were taken from study areas in aspen parklands within 150 km of EINP (Table 4-2).

Forage intake rates for each species were also taken from nearby studies. Because I lacked a complete set of seasonal forage intake rates for all species, I used mean summer and fall intake rates for bison (10.4 kg/day) and mule deer (2.3 kg/day), fall intake rates for wapiti (6.9 kg/day) (Kuzyk and Hudson 2006; Kuzyk and Hudson 2007) and annual intake rates for moose (9.9 kg/day) (Renecker and Hudson 1985) (Table 4-2).

Mass measurements of male and female bison, wapiti and moose were taken from growth curves fit to data collected at EINP (Renecker et al. 1989). Weights of white-tailed deer were obtained from field-dressed animals taken within 150 kilometers of EINP (Wishart 1984) and converted to whole animal mass measures (Harlow and Jones 1965 in Halls 1984). Gender ratios were assumed to be 50:50 males to females, giving annual average mass estimates of 615 kg for bison, 450 kg for moose, 350 kg for wapiti and 87 kg for deer.

I determined optimal combinations of ungulate numbers and ungulate biomass that were comparable to those in the park gathered from aerial surveys in December 2006 when there was snow on the ground and a lack of leaves on trees to maximize visibility (Cool 2006). I repeated the analysis using grass and forbs set at a constant level, and shrubs set at 60% utilization due to their noted resilience to herbivory (Telfer and Scotter 1975) as I reasoned that availability of shrubs to browsing ungulates would be less impeded by snow (Visscher et. al. 2006). The model solutions of optimal combinations of ungulates have an associated annual forage use for the ungulate guild, which can be used as a measure of economic carrying capacity, and thus presents opportunities for insight into carrying capacity estimates for sympatric ungulates and ungulate management options for the park.

4.3. Results

4.3.1 Stocking Strategies for Maximum Number of Individuals

Calculations were conducted with the objective of achieving maximum animal numbers in the park, for example, to maximize viewing potential. In this scenario, individuals of all ungulate species were assumed to be of equal value. A similar number of animals (972) to those observed to inhabit EINP (959) in 2006 were determined with forage use set at 7% (all forage classes) (Table 4-3). The value of 7% forage use is clearly lower than the 35% used as a minimum in other protected areas.

The result using 7% forage use also had markedly different combinations of ungulates than occurred in EINP in December 2006 (Table 4-3). While 78 deer, 72 moose and 476 bison occupied the park in 2006, the predicted optimal combination was 425 deer, 24 moose and 174 bison. Numbers of wapiti (333) were close to the predicted representation (348). When forage use was increased above 8%, moose were not prescribed by the optimal solution because shrubs were no longer available, wapiti numbers remained at the minimum population density, whereas bison and deer increased (Figure 4-3). Under this scenario, the high contribution of deer to the total numbers of ungulates is expected as deer have the lowest mass of all species considered, which can be compensated for by increased animal numbers.

Qualitative changes in the solutions were found as a function of forage usage (Figure 4-3). For forage use at 7%, bison were above the minimum viable population size, whereas wapiti were at their minimum density. For higher forage use (8% or more), moose were eliminated, wapiti remained at the minimum, and deer and bison numbers were above each species' minimum and increased markedly with increasing forage use (Table 4-3; Figure 4-3).

When I set shrub utilization at 60%, with forb and grass forage use between 7 and 15%, deer and moose dominated the system, with wapiti and bison remaining at their minimum viable numbers (Table 4-3). In the previous scenario when forage requirements for grass, forbs and shrubs were 7%, there were 425 deer, 348 wapiti, 24 moose and 174 bison, which differed when grass and forbs were 7% and shrubs was 60%, giving 246 deer and 492 moose, with the same number of wapiti and bison (Table 4-3; Figure 4-3).

4.3.2 Stocking Strategies for Maximum Biomass

The model associated 11% forage use (all forage classes) with a maximum ungulate biomass of 34.8 kg/ha, a value similar to that in EINP (33.5 kg/ha) in December 2006. At 11% forage use, the model predicted densities of bison (0.031 ha^2), moose (0.015 ha^2), wapiti (0.026 ha^2) and deer (0.0 ha^2) that differ from current EINP densities of bison (0.036 ha^2), moose (0.005 ha^2), wapiti (0.025 ha^2) and deer (0.006 ha^2) (Table 4-4).

When total forage use was 18% (ungulate biomass at 57.2 kg/ha) the solution was associated with bison and moose densities of $0.06/ha^2$ and $0.03/ha^2$ respectively, and at 25% (ungulate biomass at 79.6 kg/ha) with 0.08 $bison/ha^2$ and 0.05 $moose/ha^2$, while wapiti densities remained constant at the MVP (Figure 4-4). Deer were not present in any optimal solutions from 10 -70% forage use.

Setting maximum allowable shrub utilization to 60% and leaving grass and forbs at 7% forage use produced a total ungulate biomass of 35.2 kg/ha, which is similar to that present in EINP (33.5 kg/ha) in December 2006 (Table 4-4). When forage use of grass and forbs was set at 7-15% and shrubs at 60%, optimal stocking combinations were dominated by deer and moose, with bison and wapiti at minimum viable population levels (Table 4-4).

Sensitivity analysis for 11% annual forage use across all forage types (which results in similar biomass and ungulate configuration as that observed in the park in December 2006) indicated that an increase of 1 kg/ha of available grass and shrub forage would increase maximum ungulate biomass levels by 0.176 and 0.143 kg/ha, respectively. Given that 1 kg/ha is distributed over the spatial extent of the study area (13,400 ha), an increase of this magnitude represents an additional 2,358 kg of biomass, which is equivalent to about four additional bison for the study area. The constraint for available forbs is non-binding and increasing this forage component alone would not yield an increased ungulate biomass.

4.4 Discussion

I compared model solutions of maximum ungulate numbers and maximum ungulate biomass to recent (December 2006) observed ungulate densities in Elk Island National Park that allowed the opportunity to develop estimates of economic carrying capacity. For example, by setting the annual proportion of forage used at 7-11%, the model predicted ungulate densities comparable to those observed in the park in 2006. Assuming ungulate densities have been managed at or close to carrying capacity in the park, linear programming solutions for forage use (7-11%) are lower than those recommended by others (e.g., 35-50%) (Holechek et al. 2004). This dichotomy in forage use provides an excellent opportunity to explore the concept of carrying capacity.

4.4.1 Forage Allocation Approach

Useful models for resource managers are those that are simple and focused on a specific problem (Starfield 1996). Complex dynamic models of grazing systems can be impractical for resource managers, as they often require complex data and the services of the model developer. I used linear programming to allocate forage in an effort to maximize ungulate numbers or ungulate biomass appropriately, constrained by forage availability, sustainable use, and minimum viable populations of bison and wapiti. I assumed linearity in the model even though many problems in ecology are non-linear. For example, coefficients of forage use were fixed although they are known to vary with relative availability, snow conditions, and behavioural interactions. Linear programming is a useful tool because the method of optimizing an objective function guarantees finding the global maximum or minimum, which is rarely the case in non-linear model optimization. I also provided a protocol and template to assist adaptation to different habitats and ungulate species (Table 4-1 and Table 4-2).

4.4.2 Carrying Capacity and Allowable Forage Offtake

Estimates of carrying capacity were derived from forage use levels and comparing the model solutions (outputs of optimal combinations of ungulates), to observed densities of ungulates surveyed in the park (December 2006). I did not validate model solutions with forage utilization studies, as the aim of the study was to predict optimal combinations of ungulates so I compared model solutions with estimates of ungulate densities. Bison and wapiti densities are considered accurate as these species are contained by the fence but there may have been more moose and deer in the park at other times of year, which would remove substantial amounts of vegetation. For example, during the December survey, there were an estimated 476 bison and 333 wapiti but only 78 moose and 72 deer, which may suggest trans-boundary movements of moose and deer and be reflected in the low forage use. The large amount of water present in the park (10% of total area) may attract moose in the summer and they may stay there for part of the year. When herbage availability decreases in late fall, and wapiti switch to browse, moose may be displaced by the high density of wapiti and their "mobbing" effect (Telfer and Cairns 1986). After plants senesce in late fall and certainly during the spring flush of new vegetation, deer may move out of the park into the surrounding agricultural land to feed on agricultural crops.

The EINP ungulate survey was also based on pre-calving numbers, so forage removal by young-of-the-year ungulates would not be accounted for. I used forage intakes based on estimates gathered from experimental animals which were barren females and generally lighter than EINP animals. These factors may have lead to an underestimate of forage intake. In addition, the cost of lactation may increase forage intake by 50% (Gedir and Hudson 2000). But these measures are consistent with conventional animal-unit calculations which also ignore forage intake by calves or lactation of adult females (Holechek et al. 2004).

Previous estimates of high biomass (57.1 kg/ha) in EINP assumed intake of ungulates at 2.2 lb/100 lb body mass (Telfer and Scotter 1975). When I set forage use at

18%, model solutions were comparable to those estimates of high ungulate biomass (Telfer and Scotter 1975). Telfer and Scotter (1975) however, did not include deer in their study. I included deer in the model, which may have accounted for greater overall forage removal and the disparity between the estimate reported here, and that reported by Telfer and Scotter (1975).

The perimeter fence restricts movement of bison and wapiti, forcing them to subsist year-round on vegetation within the park. Both species are large-bodied and grass is predominant in their annual diet (91% for bison; 50% for wapiti), which is unlikely to change even if their densities increase (Singer and Norland 1994). Grass intake was the main constraint preventing increased stocking rates. This was illustrated by fixing shrub utilization to 60% (Telfer and Scotter 1975) while leaving "forage use" set at lower levels; the combination of these limitations produced a system dominated by moose and deer, and resulted in bison and wapiti abundance equal to those densities previously established to represent MVP.

The forage allocation approach does not account for forage quality and I assumed that forage quality does not limit intake. Forage quality models have been developed for mule deer (Wallmo et al. 1977), wapiti (Hobbs et al. 1982), mountain sheep (Mazaika et al. 1992), and white-tailed deer (Potvin and Huot 1983; McCall et al. 1997). Forage biomass models can be comparable to nutritional-based models when forage quality is not limiting (McCall et al. 1997). The advantage of the forage quantity approach is the limited data requirements. Although, I still did not have current annual vegetation biomass data or GIS habitat classification (1995) to compare with predicted ungulate combinations. Forage quality models still determine principle forage use from diet studies, but metabolizeable energy and nitrogen requirements need to be garnered from laboratory anlaysis. There are also still many assumptions that need to be made in forage quality models regarding nutritional requirements for each ungulate species (Miller and Wentworth 2000).

Functional interactions of ungulates (Hobbs 1996), changing vegetation succession (Barrett and Stiling 2006; Knapp et al. 1999; Fuhlendorf and Engle 2001), and dynamic feedback by ungulates to stimulate plant growth (Samson et al. 2004; Martin and Wilsey 2006; Vazquez and Simberloff 2006) were also not accommodated in this forage allocation approach. The park is generally available to all ungulates throughout the year (i.e., there are no seasonal migrations to other food sources). Bison and wapiti can show localized habitat separation in EINP (Telfer and Cairns 1986) and competition between bison and mule deer is considered insignificant (Shaw and Meagher 2000). Mule deer can favor growth of grass by browsing competing shrubs and forbs (Kay and Bartos 2000). Bison activity (wallowing, trampling) may have reduced the southern expansion of aspen trees to the prairie (Campbell et al. 1994), but the number of bison currently in the park has not reduced aspen encroachment.

Because less than 10% of park habitat contains a major component of graminoids, these areas can become heavily grazed and vegetation damaged by trampling (Bork et al. 1997b; Cumming and Cumming 2003). Heavy herbivory has been tied to reductions in the structural diversity of forest and understory strata (Bork et al. 1997a; Fornara and Du Toit 2007; Manier and Hobbs 2007), as well as replacement of native plant communities by less diverse communities dominated by introduced plant species (West 1993; Bork et al. 1997b; Vavra et al. 2007). If a large component of the herbivory is occurring in select areas of the park such as grasslands, then there may be an assumption that the entire park is being heavily grazed. Prescribed fire can alter plant communities and enhance grass biomass (Bork et al. 1997a). EINP's long-term goal for the prescribed fire program is to promote biological diversity and is not intended to increase production of grazers or browsers. A large wildfire in 2004 burned much of the Main Park. Because of this event, the prescribed fire program was put on hold for several years. It is anticipated that the program will be re-implemented in 2009, and may increase grassland habitats for bison and wapiti.

Solutions using shrub utilization of 60% and much lower fixed values for grass and forbs (7-11%) produced a system dominated by moose and deer. Browse survey data from EINP shows that beaked hazel provides over 50% of the available browse and is very resilient to browsing, with 70-80% utilization common (Best et al. 2003). However, it is uncertain whether this use is sustainable, particularly when coupled with marked reductions in the abundance of other palatable shrubs such as Saskatoon, pincherry and chokecherry within the park (Bork et al. 1997b). In addition, interpretation of forage use can be problematic with sympatric herbivores when particular forages are over- or under-used relative to their availability (Steinheim et al. 2005; Mysterud 2006).

Loss of vegetation due to weathering could have accounted for substantial reduction of available forage biomass (Hunt 1977; Willms et al. 1998) and may be a critical but un-quantified factor in estimating carrying capacity on northern ranges. In southeast Alberta on ungrazed pastures, total over-winter weathering loss to available vegetation was up to 60%, and also varied with forage class, whereby forbs could disappear almost completely while losses for grasses ranged between 27-52% (Willms et al. 1996; Willms et al. 1998). This is similar to an estimated over-winter weathering loss of 58% forage biomass at Ministik Research Station and EINP (Donkor et al. 2007). Weathering loss is greatest after senescence (Willms et al. 1998), largely because some of the vegetation can become decumbent from mechanical breakage from snow loads (Willms et al. 1998). The fragmented leaves and vegetative parts begin decomposition by weathering, leeching (Hunt 1977), photochemical processes (Moorhead and Reynolds 1989) and microbial degradation (Holland and Coleman 1987). Moisture, temperature and wind can enhance vegetation decomposition rates, as experiments monitoring cotton rotting rates found high decomposition rates during wetter seasons and were associated with microhabitats such as wetter slopes (Risch et al. 2007).

The forage allocation approach used here does not explicitly account for diet quality restrictions, nor changes in biomass availability with depletion. The availability of seanonal biomass and nutritional quality are not monitored and the research necessary to turn these measures into an assessment of the nutritional adequacy is therefore incomplete. This problem is handled by allowing an additional reduction in the safe-use factors, which may reduce but not eliminate this risk. Ungulates select the most nutritious forage initially and use this selection opportunity as it is progressively depleted.

4.4.3 Management Challenges

For resource managers, impacts from ungulates on vegetation are becoming a common management problem (Decalesta 1994; Allombert et al. 2005a,b; Anderson et al. 2007; Johnston et al. 2007; O'Connor et al. 2007; Landman et al. 2008), while options for controlling ungulate populations by slaughter, translocation and reproductive control receive little public and/or government support (Gogan et al. 2001). Translocation receives the greatest level of public support, but disease concerns have reduced the safety of translocating wildlife (Bellhouse and Rosatte 2005; Brooks and Hoberg 2006; Sibley et al. 2007). Along with the high costs of handling and management, resource managers have explored alternatives for vegetation management including prescribed burning (Bork et al. 1997a; Negron-Ortiz and Gorchov 2000; Van Dyke and Darragh 2006; Petty et al. 2007) and intra-guild competition (Blyth and Hudson 1987; Blyth 1995; du Toit and Yetman 2005; Makhabu et al. 2006).

Properly applying carrying capacity is essential to dealing with management problems for ungulates and vegetation. When the concept of carrying capacity was initially developed in wildlife and range management, estimates of forage removal by ungulates were commonly set at 50% under moderate grazing (Stoddard and Smith 1955). Recently, more conservative levels of forage removal are being considered in an attempt to account for abiotic factors such as droughts (McLeod 1997) and biotic factors such as trampling (Holechek et al. 2004). Some authors have suggested setting carrying capacity at 25% forage removal by the target ungulates, which would leave 25% for natural disappearance by other wildlife, insects, trampling and weathering and the remaining 50% for site protection (Holechek et al. 2004). In a detailed evaluation of stocking rates for livestock, Galt et al. (2000) determined that measured forage use was consistently 10-15% greater than intended use. A significant problem associated with estimating carrying capacity is related to the time and labor required to annually estimate forage biomass. As a consequence, lack of attention to these factors can lead to errors in stocking rates and potential problems with range overuse and land degradation (Dijkman 1993; Holechek et al. 2004).

In this study, weathering losses of forage may explain the apparently low proportion of forage used by the four ungulate species. Reduced availability of forage due to weathering loss is rarely assumed as a separate category, and is normally pooled with other losses such as consumption by other wildlife species (including insects), and trampling. Under these assumptions, pooled losses in this category are generally assumed to be 25% combined (Holechek et al. 2004). The study areas where weathering loss has been pooled with other losses are from arid and semi-arid regions in the United States (Holechek et al. 2004), which differs climatically and topographically from EINP. The EINP study area contained about 10% standing water, and receives precipitation in the form of both rain and snow. Water is a key component in weathering loss to vegetation as it can increase decomposition rates through microbial action (Hunt 1977). Snow pack can mechanically break vegetation, and during the spring melt the ground layer over a larger percent of the park may be moist, adding to decomposition rates (Risch et al. 2007). In addition, because a large component of grasses and sedges sought by bison and wapiti are near water bodies, vegetation that is trampled may be exposed to moist soil, with increased susceptibility to decomposition.

If annual weathering losses of grasses in Alberta are found to be near 50% (Donkor et al. 2007), or between 27-52% depending on grass species (Willms et al. 1998), then this loss should be taken into account for annual estimates of carrying capacity in EINP. In addition, wildlife managers must take into account the amount of forage available to ungulates for an entire year, in contrast to range mangers who do not need to account for winter weathering losses because livestock are removed from the range after plants senescence. Although Irby et al. (2002) created a forage allocation model for wild ungulates in a National Park in North Dakota and assumed 35% forage use, they provided no results or discussion of total annual forage removal and thus avoided explaining implications for wild ungulates during one full year. My study provides a template for the initial estimate of stocking combinations for subsequent refinement and long term programs of adaptive management..

Table 4-1. Estimate of forage production (kg/ha) within each of four primary habitats in Elk Island National Park, Alberta.

Habitat classification	Area (% total)	Grass	Forb	Shrub	Total
Aspen/balsam popular upland	0.60	247[a]	399[a]	1053[a]	1699
Upland grass/shrub	0.17	3120[b]	746[c]	86[c]	3952
Wetland sedge/shrub	0.10	6053[b]	470[c]	11[c]	6534
Coniferous mixedwood	0.02	9[c]	185[c]	461[c]	655
Water	0.11	-	-	-	-
Total forage		1284	417	657	2358

[a] Best and Bork 2004

[b] Bork et al. 2001

[c] Willoughby et al. 2006

Table 4-2. Diet composition and total annual intakes of major forage classes for one individual for each of four ungulate species in the aspen boreal forest zone of Alberta.

	Spring (% diet)			Summer (% diet)			Fall (% diet)			Winter (% diet)			* Total Annual Intake (kg/hd/yr)			
	Grass	Forb	Shrub	Grass	Forb	Shrub	Grass	Forb	Shrub	Grass	Forb	Shrub	Grass	Forb	Shrub	Total
Bison	96[a]	4[a]	0[a]	75[b]	25[b]	0[b]	98[c]	1[c]	1[c]	96[a]	0[a]	4[a]	3454	304	38	3796
Moose	0[e]	2[e]	98[e]	1[d]	47[d]	52[d]	12[d]	0[d]	88[d]	3[ae]	6[ae]	91[ae]	145	506	2963	3614
Wapiti	92[a]	3[a]	5[a]	8[e]	25[e]	67[e]	64[e]	3[e]	33[e]	38[ae]	4[ae]	58[ae]	1259	227	1033	2519
Deer	94[a]	1[a]	5[a]	36[c]	7[c]	57[c]	51[c]	6[c]	43[c]	23[af]	4[af]	73[af]	420	42	378	840

[*] kg/hd/yr = (mean annual diet x daily forage intake x head x 1 year)

[a] Cairns 1976

[b] Holsworth 1960

[c] P. Dewitt, unpublished data.

[d] Renecker 1987a

[e] Renecker 1987b

Table 4-3. Comparison of maximum animal numbers within Elk Island National Park in 2006 to model predictions based on percentage (%) forage use. Forage use is defined as equivalent ratios of grass, forbs, and shrubs except when grass and forbs were equivalent and shrubs were set at 60%.

		7% Herbage Use		11% Herbage Use		15% Herbage Use	
	EINP	7% Shb	60% Shb	11% Shb	60% Shb	15% Shb	60%Shb
# animals	959	972	1260	2039	3268	2976	5275
Density/ha	0.07	0.07	0.09	0.15	0.24	0.22	0.39
Bison	476	174	174	265	174	374	174
Moose	72	24	492	0	792	0	1092
Wapiti	333*	348	348	348	348	348	348
Deer	78	425	246	1425	1953	2254	3660

* Wapiti numbers in 2006 were below their Minimum Viable Population.

Table 4-4. Comparison of maximum ungulate biomass of Elk Island National Park stocking rates (2006) with model predictions based on percentage (%) forage use. Forage use is defined as equivalent ratios of grass, forbs, and shrubs except when grass and forbs were equivalent and shrubs were set at 60%.

		7% Herbage Use		11% Herbage Use		15% Herbage Use	
	EINP	7% Shb	60% Shb	11% Shb	60% Shb	15% Shb	60% Shb
kg/ha	33.5	21.9	35.2	34.8	56.3	47.6	77.5
Density/ha	0.07	0.05	0.09	0.07	0.24	0.10	0.39
Bison/ha	0.04	0.02	0.01	0.03	0.01	0.05	0.01
Moose/ha	0.01	0.01	0.04	0.01	0.06	0.02	0.08
Wapiti/ha	0.02	0.03	0.03	0.03	0.03	0.03	0.03
Deer/ha	0.01	0.00	0.02	0.00	0.15	0.00	0.27

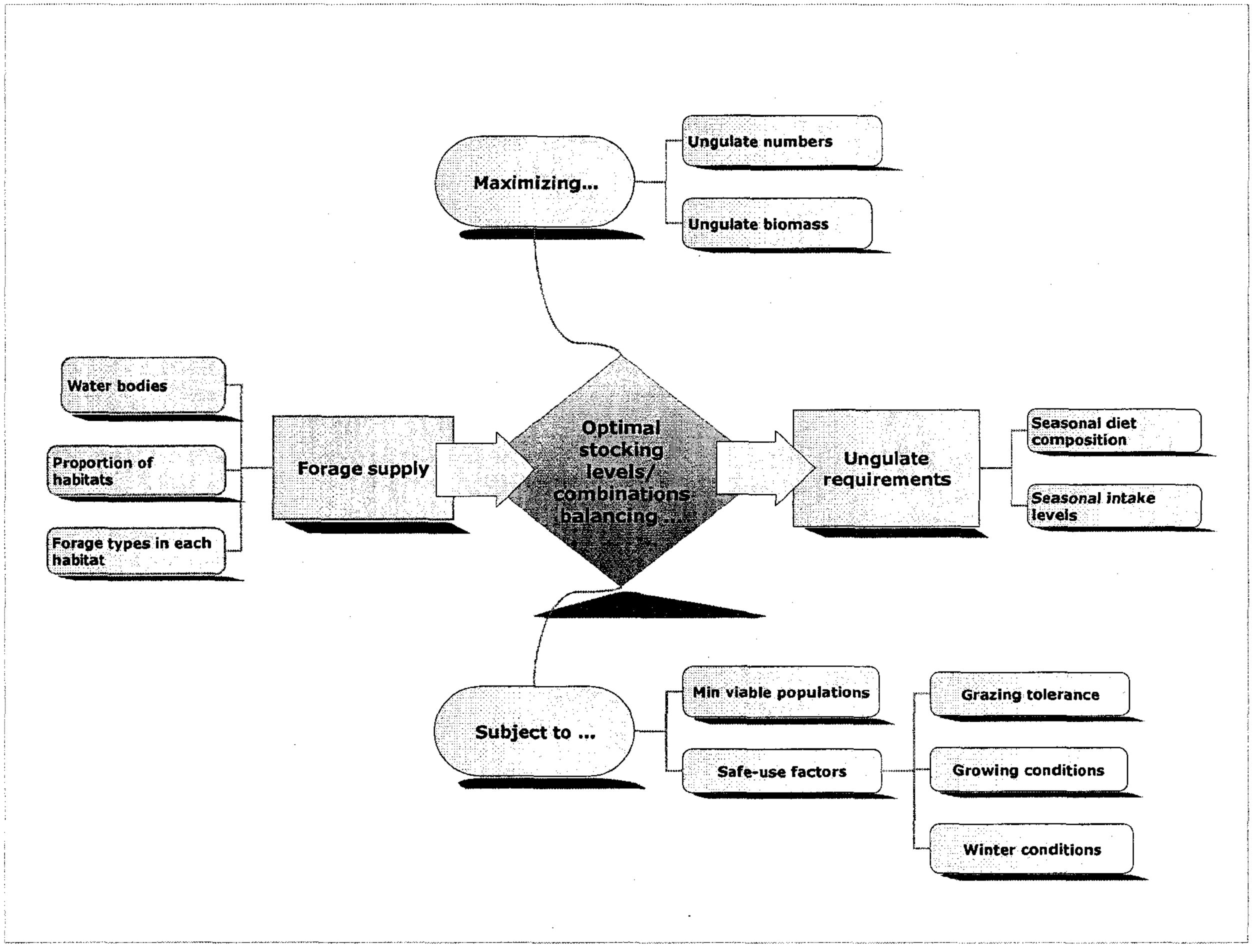

Figure 4-1. Aggregate forage supply and demand factors for ungulates in fall of 2006 in Elk Island National Park, Alberta.

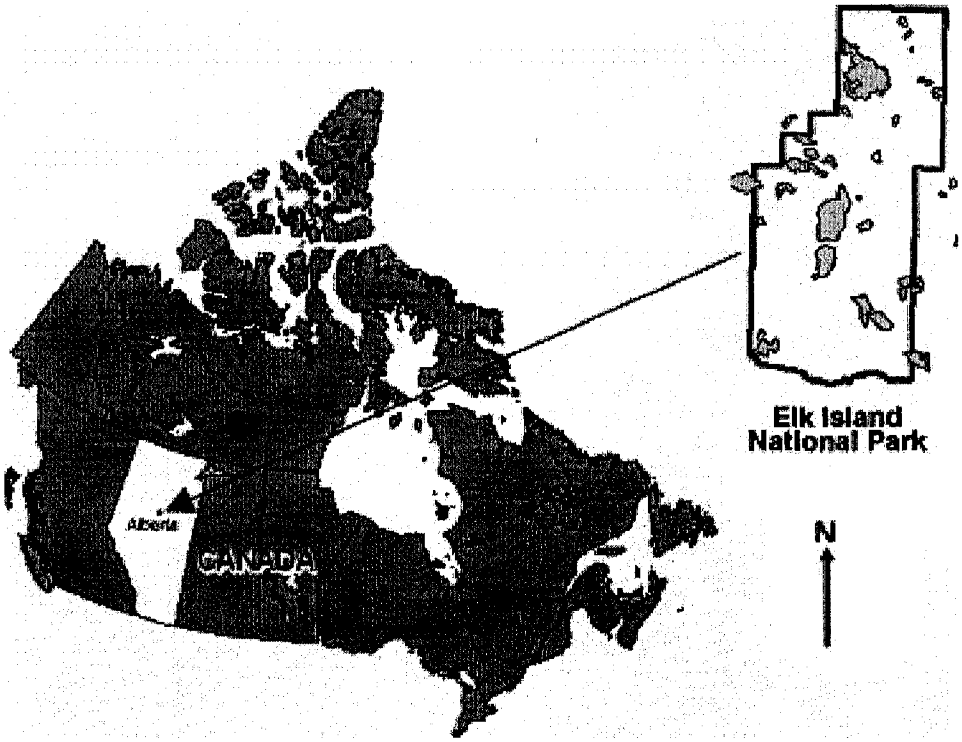

Figure 4-2. Location of Elk Island National Park in central Alberta, Canada (Map courtesy of Parks Canada).

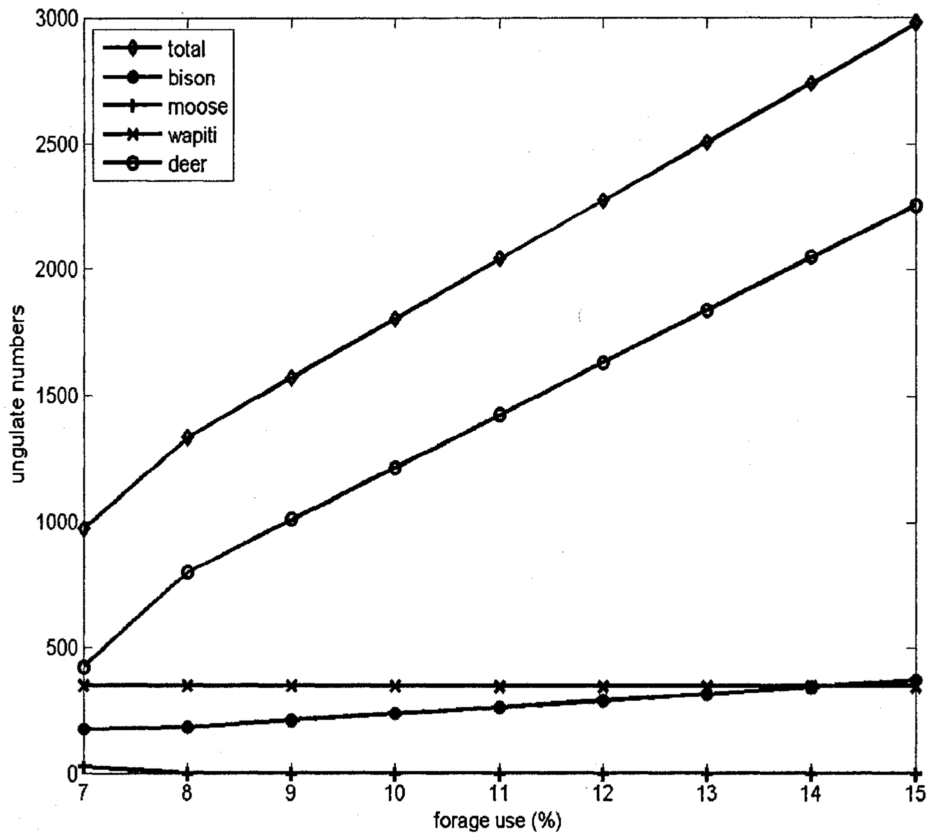

Figure 4-3. Results from the forage allocation model to maximize animal numbers in Elk Island National Park. Ungulate numbers are shown for all and each species separately. For all forage usages, wapiti remain at their minimum viable population level, with bison and deer increasing with increasing forage. Moose are only present for a narrow range of forage usage.

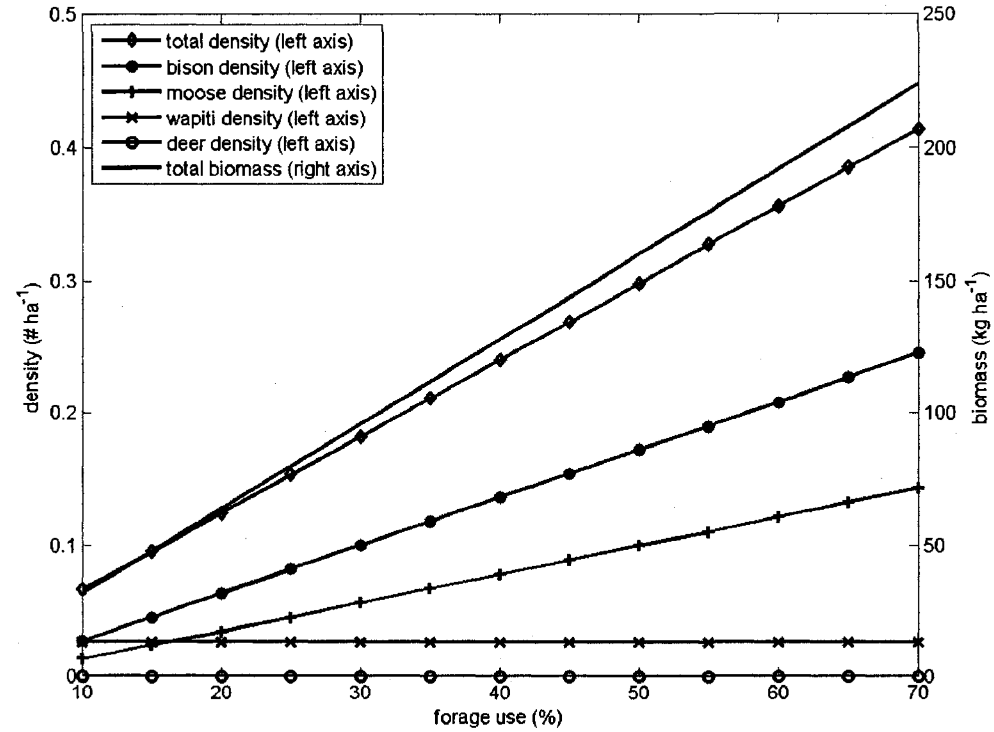

Figure 4-4. Results from the forage allocation model to maximize biomass in Elk Island National Park, subject to the constraints of forage availability and minimum viable population densities for bison and wapiti. Ungulate densities and total biomass are shown for a range of percent forage use. Total density and total biomass increase with increasing forage use. Bison and moose densities also increase with forage use. Deer density is zero for all forage use whereas wapiti density remains at the minimum set by the minimum viable population constraint.

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Chapter 5. Synthesis

This thesis provides a framework and template for estimating carrying capacity for sympatric ungulates. Applying the concept of carrying capacity to the management of ungulates has been occurring for decades (Leopold 1933; Georgiadis et al. 2007), yet many have questioned the validity and practicality of estimating carrying capacity and using it as a management tool (Bell 1986; Dhondt 1988; Dijkman 1993; McLeod 1997; Miller and Wentworth 2000; Morris and Mukherjee 2007; Sayre 2007). I dealt with carrying capacity as a concept that is commonly used to describe interactions between ungulates and vegetation (Seidl and Tisdell 1999; Roy and Thomas 2003; Mysterud 2006), yet found definitions imprecise (McNab 1985; Miller and Wentorth 2000) and that in practice carrying capacity was rarely estimated (Price 1999; Holechek et al. 2004; Morris and Mukherjee 2007; Morellet et al. 2007; Reid et al. 2007).

Despite ambiguities in definitions and lack of precise methodologies, I chose to confront the challenge of estimating carrying capacity because there is continued interest in ungulate-vegetation interactions, and a need for resource managers to implement sustainable forage use by ungulates (Palmer et al. 2003; Choquenot and Ruscoe 2003; Gordon et al. 2004; Grange and Duncan 2006; Tremblay et al. 2007; White et al. 2007; Bolger et al. 2008). For example, emphasis has been placed on implementing the concept of carrying capacity for long-term sustainability of rangelands (Tewari and Arya 2005; Benjaminsen et al. 2007; Brekke et al. 2007; Hayward et al. 2007) and as a planning tool in large land-use initiatives. In Africa, grazing restrictions have been applied and cattle destocked according to a theoretical carrying capacity in an attempt to reduce desertification (Pearce 1992). In addition, there are several recent studies on overabundant wild ungulates impacting vegetation (Côté et al. 2004; Brathen et al. 2007; Morellet et al. 2007; Bradford and Hobbs 2008) but with only limited focus on carrying capacity (Irby et al. 2002; Mysterud 2006). There have been estimates of carrying capacity developed for mule deer (Wallmo et al. 1977; Albert and Krausman 1993), white-tailed deer (Potvin and Huot 1983; Harlow 1984; McCall et al. 1997), wapiti (Hobbs et al. 1982), moose (Crete 1989), and mountain sheep (*Ovis canadensis*) (Mazaika et al. 1992) but estimates for multi-species systems are rare (Hudson and Blyth 1986; Irby et al. 2002) and must be based on different principles.

I advanced knowledge toward the concept of carrying capacity for multi-species ungulate systems. I began by using a precise definition of economic carrying capacity (Caughley 1979) and a one-year time step to align with the scope of mangement interests, and to provide realistic management scenarios based on short-term ungulate densities and available resources (McLeod 1997). I incorporated the theory on relationships between ungulates and vegetation (Leopold 1933, Caughley 1979; Pastor et al. 1997; del Monte-Luna et al. 2004; Van der Graaf et al. 2005; Gillson and Hoffman 2007; Hansen et al. 2007; Tremblay et al. 2007) to formulate an appropriate direction for developing to a carrying capacity estimate for a multi-species ungulate system (Chapter 1).

Due to the challenge of gathering the required information, there are still problems implementing theoretical aspects of carrying capacity in field research (Dijkman 1993; McLeod 1997; Cumming and Cumming 2003; Georgiadis et al. 2003; King and Gurnell 2005). Therefore, I began my research by refining daily DMI rates that are crucial parameters for reliable carrying capacity estimates (Wallmo et al. 1977; Potvin and Huot 1983; Hobbs and Swift 1985; McCall et al. 1997; Irby et al. 2002; Chamaille-Jammes et al. 2008). I applied a novel technique (*n*-alkane ratio technique) to refine the practical problem of estimating DMI for mule deer, as their broad diet selection created several challenges to the technique (Chapter 2) (Kuzyk and Hudson 2006). Because most ungulate systems contain multiple species, I then estimated concurrent forage intake rates for mule deer, wapiti, and bison (Kuzyk and Hudson 2007). These intake estimates for multiple species are essential for carrying capacity estimates, yet such information is rare in the literature (Holechek et al. 2004).

My estimates of DMI from the paddock-level experiments (Chapters 2 and 3) are incorporated in the forage allocation model for an ungulate guild, which is the quantitative synthesis for the thesis (Chapter 4). Chapter 4 is the thread that incorporates theoretical concepts of carrying capacity into a comprehensive forage allocation model that can be easily used by managers. The forage allocation model covers theoretical considerations of carrying capacity, and has a practical component where Tables 4-1 and 4-2 provide templates for resource managers, which can be modified to estimate carrying capacity for a diversity of multi-species grazing systems.

I chose to estimate carrying capacity for an ungulate guild in a protected area that was enclosed by a fence and lacked predators. There are similar areas around the globe which also have high densities of ungulates and few predators (Woodruffe and Ginsberg 1998; Hayward et al. 2007). In addition, fences have been placed around protected areas to exclude unwanted predators (Moseby and Read 2005; Hadwen et al. 2007; Robley et al. 2007), but the fences also restrict movements of ungulates that normally migrate (Ward et al. 1999; Berger 2004) leaving a need to link protected areas to the surrounding landscape (Hansen and DeFries 2007; DeFries et al. 2007). As such, the lack of predators, issues with fenced ungulates and the need to intergrate management descisions with surrounding landscapes made EINP an ideal site to research carrying capacity.

The integration of these thesis chapters has produced a carrying capacity estimate for sympatric ungulates and provided a sound opportunity to extend this work to other systems (Harrington and Conover 2006; Larson and Paine 2007; Pringle et al. 2007). Although I developed the application for four ungulates in central Alberta, these templates can easily be applied to other systems with similar problems. I extended the animal-unit concept to an animal-unit-year approach and developed templates that can be used as a practical application for similar problems.

In a recent review on the global perspective of ungulate conservation and management, Gordon et al. (2004) pointed out a common disjunct between researchers and managers and they suggested that academics and managers work together to examine problems such as ungulates and "carrying capacity". I have accomplished this goal by working directly with resource managers in EINP to build on previous knowledge and integrate ecological theory, in developing an estimate of carrying capacity that can be used by all. I did this using my thesis chapters (Kuzyk and Hudson 2006; Kuzyk and Hudson 2007; Chapter 4) as a framework to build and develop an overall structure that has advanced both the theory and implementation of carrying capacity for ungulates in a multi-species system.

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Appendix 1.

Twenty-Four-Hour Activity Budgets of Mule Deer in the Aspen Parkland of East-central Alberta

Introduction

Mule deer range over much of western North America, yet little in known about their foraging ecology on northern ranges (Kuzyk and Hudson 2007), especially regarding their daily activities. Documenting how much time mule deer spend feeding during different stages of vegetation phenology provides insight into behavioral adaptations in seasonal northern environments. Browsing ruminants normally spend about 50% each day foraging, with feeding times varying with forage phenology, morphological and physiological characteristics such as mouth shape, gut capacity and food passage rate (du Toit and Yetman 2005). Activity budgets can be used to quantify daily foraging times and other major activities. One difficulty in conducting activity budgets is remaining close enough to a focal animal to accurately quantify activity patterns, especially during darkness. Using tame deer is one way to maintain consistent visual contact with a focal animal for a 24-h period (Collins and Urness 1983) and provides reliable results, as food intake in tame deer is deemed innate (Spalinger et al. 1997). Maintaining visual contact with tame deer also allows quantifying daily feeding cycles and duration of feeding bouts.

The purpose of this study was to quantify activity budgets of mule deer on northern ranges when the vegetation was green (June and July), maturing (September) and cured (October). From allometric considerations (Mysterud 1998; du Toit and Yetman 2005), we predicted that mule deer would spend 50% of their daily activity budget foraging and foraging time would change with forage phenology. We predicted that mule deer would spend the least time foraging in summer when vegetation was green and the most time in autumn when the vegetation had cured because required selectivity increases search time.

Methods

Our study animals were two unbred adult mule deer does which were hand-reared as fawns. The animals were four and six years old and weighed 59 and 60 kg at the beginning of the study. These animals would allow researchers to remain within 5 m of them without disturbing their normal activities. The deer were released into 3-7 ha fenced enclosures (2.2 m high) in an aspen parkland habitat (Strong 1992) at the University of Alberta Ranch (53°N, 111°31'W) approximately 150 km southeast of Edmonton, Alberta. Each deer was instrumented with a radiocollar (Telonics TGW-3570) and placed in a paddock with two other mule deer as part of a larger study (Kuzyk and Hudson 2006). This study was approved by the University of Alberta Faculty Animal Policy and Welfare Committee (Protocol HUDS 2004–33B), following guidelines of the Canadian Council on Animal Care.

Scan sampling (Altmann 1974) was conducted on focal deer throughout one complete 24-h period and repeated seven times during the summer and autumn of 2004 and 2005 (Table A1). One mule deer (501H) was used for six of the sampling periods (July 2004 and 2005, September 2004 and 2005, October 2004, June 2005) and was substituted for another mule deer (515K) in October 2005 to compare behaviors at the same season but different years (Table A1). Only one 24-h activity budget was conducted per sampling period. The activity budget was classed into predominant activities and recorded every 10 min (Collins and Urness 1983). One observer closely followed the deer and used a stopwatch to time predominant activities within a ten-min bout. A predominant activity had to occur for five min or longer within a ten-min time interval to be classed as predominant. Predominant activities were feeding, bedding, walking and other (social interactions, grooming). Feeding was defined as ingesting, chewing or intently searching (smelling plants) for food, whereas walking was a deer moving without biting vegetation. Ruminating was associated with bedding. Each observer spent between 6 and 10 h with the mule deer and overlapped shifts by approximately 15 min to minimize disturbance to the deer. At night, a flashlight was used to monitor the mule deer by concentrating the light beam on the posterior portion of the body to minimize disturbance.

Daily patterns of feeding and bedding were determined by the number and duration of bouts (Pépin et al. 2006). Daily feeding cycles were evaluated by the proportion of time spent feeding each hour over a 24-hr period. The proportion of time spent feeding at dawn and dusk was determined by the mean amount of time spent feeding 1-3 hours before, 1 hour before and 1 hour after, and 1-3 hours after sunrise and sunset (Colman et al. 2001). Descriptive analyses of activities are presented due to insufficient sample sizes for statistical comparisons.

Results

Mule deer spent about 40% of each day foraging with slight increases when the vegetation was green and maturing (40-47%) and less time when the vegetation was cured (38-39%). Mule deer spent between 33-53% of each day bedded (Table A1). Feeding bouts were generally shorter (37-68 min) than bedding bouts (69-133 min) and there were more feeding bouts (10-16/day) than bedding bouts (4-10/day) per day (Table A2). Feeding cycles were polycyclic (Figure A1) with increased feeding activity near sunrise and sunset (Figure A2).

Discussion

Our research documents and compares daily foraging activities of mule deer on northern ranges when the vegetation was at three phenological states and deer were at successive stages of their annual growth cycle. Our findings did not meet our prediction that mule deer would spend less time foraging in summer than in autumn. We assumed abundant forage quantity and quality would account for reduced foraging activity in summer, but early summer is the period when weight gain and appetite are greatest despite the absence of milk production for fawns. We found mule deer spent more time foraging in June and July (40-47%) and September when vegetation was maturing (45%) and the least amount of time in October when the vegetation had cured (38-39%). Possibly mule deer were being very selective in forage quality in the summer period and spent more time consuming the easily digestible forbs when they were readily available. In September, mule deer may have increased foraging times as the vegetation started to senesce and deer spent more time searching for green vegetation, especially forbs beneath the grass layer.

Mule deer spent the least time foraging in October when the vegetation had cured. This may be due to mule deer adjusting their bite sizes (Kuzyk and Hudson 2006) to compensate for the lack of green vegetation. Mule deer on northern ranges have high consumption rates (g/min) in October and can forage at rates that are near theoretical maximum by feeding on Canada thistle (Kuzyk and Hudson 2006). Increased bite sizes in October could lead to a quicker gut fill compared to other seasons.

The percentage of time mule deer bedded each day equaled or exceeded that of the time spent foraging. High diurnal temperatures can reduce mule deer activity (Hayes and Krausman 1993) especially during midday (Ager et al. 2003) and could account for the difference. Beir and McCullough (1990) found that white-tailed deer were relatively inactive in summer when feeding on abundant forage. In this study, the least amount of time spent bedding was in September (32.5-38.3%) and October (36.7%). The least number of bedding bouts (4 - 7/day), and the longest in duration also occurred in September (110 - 118 min) and October (109 - 133min). Long bedding bouts may reflect requirements for rumination of coarse forage. During all seasons, there were fewer bedding bouts (4-10/day) than feeding bouts (10-16/day) and time spent bedding was longer (69-133 min) than feeding bouts (37-68 min).

There was variation in behaviors between the two mule deer in October in different years. Time spent foraging was almost identical (38.3-38.8%), whereas the time spent bedding contrasted greatly as the individual used in multiple trials (501H) spent 36.7% of the day bedding compared to 52.9% for the other individual (515K). Also, 501H spent substantially more time walking (24%) than did 515K (7%), which may be due to individual variations in behaviors.

Mule deer had polycyclic feeding cycles, which have been documented for other northern ungulates (Colman et al. 2001). The cycles may be driven by rumen fill and time required for digestion (Pérez-Barbería and Gordon 1999), as these mule deer experienced little disturbance and few intra-specific interactions (Kuzyk and Hudson 2006). Mule deer increased feeding activity near sunrise and sunset, which is similar to the behavior of white-tailed deer (Beir and McCullough 1990), as crepuscular activity is a common behavior for small ruminants to reduce predation risk (Pérez-Barbería and Gordon 1999). Additional studies quantifying activity budgets of mule deer would help clarify factors determining daily feeding cycles.

Table A1. Activity budgets (24-h) for one mule deer doe (501H) at the University of Alberta Ranch, Kinsella, Alberta.

Date	Feeding		Bedding		Walking		Other	
	% day	hrs	% day	hrs	% day	hrs	% day	hrs
2005 June 9	40.8	9.8	50.0	12	6.3	1.5	2.9	0.7
2004 July 13	41.7	10	47.9	11.5	6.3	1.5	4.2	1
2005 July 7	47.1	11.3	47.1	11.3	3.3	0.8	2.1	0.5
2004 September 11	45	10.8	32.5	7.8	21.7	5.2	0.8	0.2
2005 September 9	44.6	10.7	38.3	9.2	15.8	3.8	1.3	0.3
2004 October 8	38.8	9.3	36.7	8.8	23.8	5.7	0.8	0.2
*2005 October 12	38.3	9.2	52.9	12.7	7.1	1.7	2.1	0.5

* Note: Different mule deer (515K).

Table A2. Number and duration (mean min/bout ± SE) of feeding and bedding bouts for one mule deer doe (501H) during 24-h periods at the University of Alberta Ranch, Kinsella, Alberta.

	Feeding		Bedding	
	Bouts/24-hr	Min/bout	Bouts/24-hr	Min/bout
2005 June 9	16	36.9 ± 5.5	10	72.0 ± 16.5
2004 July 13	15	40.0 ± 8.7	10	69 ± 11.6
2005 July 7	10	68.0 ± 10.6	6	113 ± 15
2004 September 11	12	54.2 ± 11.5	4	117.5 ± 29.3
2005 September 9	11	58.2 ± 11.3	5	110 ± 27.6
2004 October 8	13	43.1 ± 9.0	4	132.5 ± 41.7
*2005 October 12	12	45.8 ± 9.4	7	108.6 ± 11.0

Note: Different mule deer (515K).

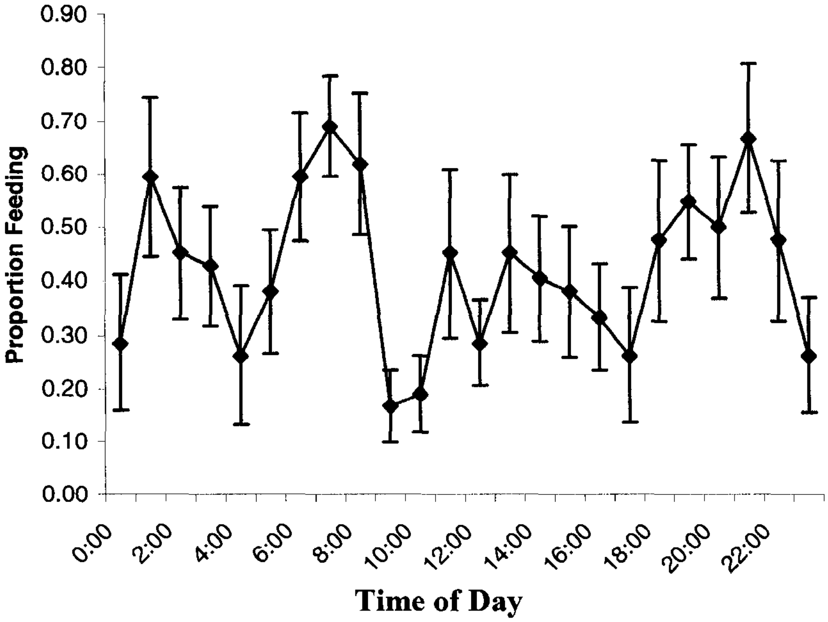

Figure A1. Feeding cycles of adult mule deer does in the aspen parkland of east-central Alberta. Data are averaged and pooled across season (June, July, September, October) and years (2004-2005).

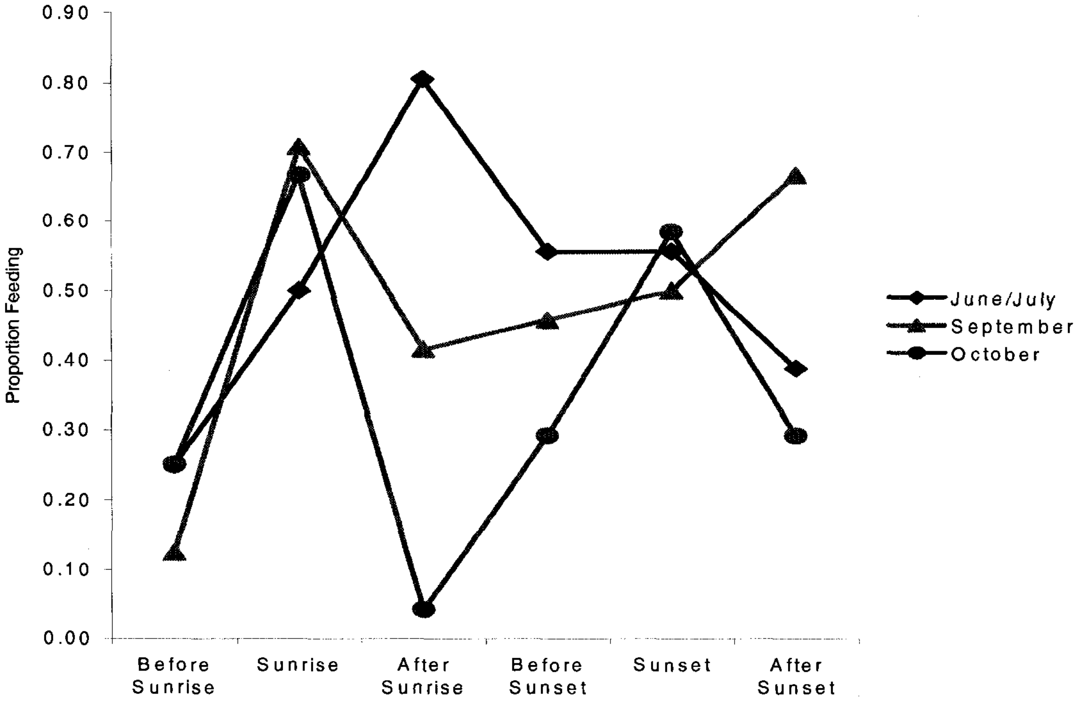

Figure A2. Proportion of time a mule deer doe spent feeding 1-3 hours before, 1 hour before and after, and 1-3 hours after sunrise and sunset in the aspen parkland of east-central Alberta. Data are averaged and pooled for season and years (2004-2005).

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