

ACTIVITY PATTERNS, FORAGING ECOLOGY, AND SUMMER RANGE CARRYING CAPACITY OF MOOSE (*ALCES ALCES SHIRASI*) IN ROCKY MOUNTAIN NATIONAL PARK, COLORADO

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ABSTRACT: To ensure sustainable populations of native animals and plants, managers of protected areas must understand carrying capacity of large wild herbivores. Estimates of carrying capacity and how large herbivores may influence native vegetation require knowledge of their activity and foraging patterns. Therefore, we examined activity patterns and foraging behavior of adult male moose (*Alces alces shirasi*) in Rocky Mountain National Park, Colorado by following individual animals and counting bites during the summer and fall of 2003 and 2004. Mean active time per day peaked in late June at 11.3 h and declined to 8.9 h in early fall preceding the breeding season. Moose averaged 6.7 feeding periods/d, each lasting 79 min; feeding bouts were longer around sunrise and sunset and were shorter midday presumably because of high ambient temperature. Activities associated with feeding and resting constituted 94.0% of daily time budgets. Feeding declined and social behavior and movement increased in fall with the onset of the breeding season. Food consumption increased steadily through early summer peaking at 126.8 g/kg BW^{0.75} in early August, followed by a sharp decline to a low of 69.1 g/kg BW^{0.75} in early September. Daily digestible energy intake was estimated at 1191 kJ/kg BW^{0.75}/d. Maximum rates of instantaneous intake were recorded in early August at 22.3 g/min. Because intake rates of willow (*Salix* spp.) increased from June-August, but nutritional quality peaked in mid-June, increases in daily and instantaneous intake rates during summer seemed more related to forage availability than protein and energy content of willow leaves. The nutritional carrying capacity of summer range in Rocky Mountain National Park in 2004 was estimated from the range supply of metabolizable energy, digestible energy, and available nitrogen. Based on the digestible energy intake and energy requirements of a 344 kg male moose, the summer range carrying capacity was estimated at 0.21 moose/km². Nitrogen based estimates were considerably higher at 0.32 moose/km².

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Because hunting is prohibited and large carnivores are rare in many protected areas in the world, resource managers are concerned about the potential effects of large populations of wild herbivores on sensitive plant species (Schreiner et al. 1996, Baker et al. 1997, Augustine and McNaughton 1998). The United States National Park Service (NPS) states that natural processes should be relied upon to the

greatest extent possible to regulate ungulate populations (NPS 2001). However, the policy is flexible resulting in varied management approaches in different situations. Where natural controls have been altered by human activity, unnatural concentrations of ungulates may be managed by park staff (Huff and Varley 1999). The number of Rocky Mountain elk (*Cervus elaphus*) in the eastern portion of the Rocky

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Mountain National Park (RMNP) in Colorado was artificially reduced in 1943-1968 in an attempt to maintain the herd at about 500 (Wright 1992). Since 1968, elk have no longer been controlled within RMNP and the population has increased substantially and been implicated in the decline of the abundance, distribution, and stature of riparian willow (*Salix* spp.) and upland shrub communities in the eastern portion of RMNP (Singer and Zeigenfuss 2002). More recently, managers have expressed concern for the health of riparian willow communities in the western portion as a consequence of a presumed increase in moose (*Alces alces shirasi*).

Understanding how many herbivores a given ecosystem can sustain and maintain ecological integrity (i.e., carrying capacity, K) is an important, yet often elusive and difficult goal for resource managers (Caughley 1979, Hobbs and Swift 1985, Regelin et al. 1987, Boyce 1989). For wild ungulates that rely on plants that vary greatly in quality and abundance both temporally and spatially, carrying capacity based on nutritional needs is generally measured as the ratio of nutrient supply of the range to the nutrient requirement of the animal (Wallmo et al. 1977, Hobbs et al. 1982, Potvin and Huot 1983), and often integrates information on food habits, daily intake, and the forage production of a given area (Crete 1989, Kufeld and Steinert 1990, Zheleznov-Chukotsky and Votashova 1998). However, these methods require accurate measures of seasonal changes in intake, diet selection, and forage production. Previous studies with moose have examined differences in seasonal dry matter intake (DMI) among seasons (Schwartz et al. 1984, Renecker and Hudson 1985, Hubbert 1987), but the dynamics within seasons has received less attention.

Most estimates of K for ungulate populations have focused on winter ranges (Hobbs et al. 1982, Potvin and Huot 1983, Crete 1989, MacCracken et al. 1997) because winter food supply is considered the limiting factor

of northern ungulates (Crete 1989, Kufeld and Steinert 1990, MacCracken et al. 1997, Zheleznov-Chukotsky and Votashova 1998), especially moose (LeResche and Davis 1973). However, ecologists are increasingly focusing their attention on forage availability and K of summer and autumn ranges (Hett et al. 1978, Beck and Peek 2001, Beck et al. 2006). Summer is a key period in which moose recover and build fat reserves for fall breeding and winter survival (Schwartz et al. 1988b), and body condition in fall has been linked to pregnancy rates (Testa and Adams 1998). Moose enter winter with an estimated 20-26% body fat (Schwartz et al. 1988b) which is critical because winter diets are insufficient to meet nutrient requirements and moose enter energy deficit. Although summer diets of moose are typically 1.5-3 times more nutritious than winter diets (Schwartz 1992), warm summer temperatures may restrict the time large-bodied ungulates forage (Taylor and Maloiy 1970, Van Soest 1982, Hudson and White 1985, Owen-Smith 1998); for example, Renecker and Hudson (1986a) measured reduced intake rate and loss of body weight during warm summer periods. Summer habitat of poor quality and/or increasing summer temperature due to global climate change may represent limiting factors in how moose prepare for and survive winter regardless of availability and quality of winter forage.

Despite the importance of summer nutrition for moose populations, and the influence of high ambient temperatures on moose foraging behavior, few studies have examined the foraging ecology, activity patterns, and K of an area for moose in summer. The objectives of this study were to 1) examine activity patterns and foraging behavior of free-ranging male moose during summer and fall in RMNP, 2) investigate the relationship between ambient temperature and daily activity budgets, and 3) use these data with nutritional and metabolic information from the literature to estimate the nutritional carrying capacity of summer range

for moose in RMNP.

STUDY AREA

This study was conducted during summer-early fall in 2003 and 2004 in RMNP that is located in north-central Colorado, covering 1,075 km² at 2,389-4,345 m elevation; RMNP lies astride the continental divide with different climates on the west and east sides. We conducted this study on the west side within the Colorado River Drainage, an area covering 390.8 km². Annual precipitation ranges from 37.6-51.7 cm with a temperature range of 24° C in July-August and -17° C in December-February (Monello and Johnson 2003).

Lower elevation riparian meadows are characterized by large stands of geyer willow (*Salix geyeriana*), mountain willow (*S. monticola*), drummond willow (*S. drummondiana*), plane-leaf willow (*S. planifolia*), and smaller stands of whiplash willow (*S. lasiandra*) and wolf willow (*S. wolfii*). Other common species are beaked sedge (*Carex utriculata*), bog birch (*Betula glandulosa*), mountain alder (*Alnus incana*), marsh reed grass (*Calamagrotis canadensis*), western dock (*Rumex aquaticus*), white clover (*Trifolium repens*), and strawberry (*Fragaria ovalis*). These areas are surrounded by stands of ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), quaking aspen (*Populus tremuloides*), and narrowleaf cottonwood (*P. angustifolia*). Higher elevation meadows are characterized by large stands of plane-leaf willow, wolf willow, and bog birch; surrounding trees include quaking aspen, lodgepole pine (*Pinus contorta*), and subalpine fir (*Abies lasiocarpa*) (Beidleman et al. 2000).

METHODS

We directly observed and measured activity patterns and foraging behavior of moose at close range (5-20 m) because moose in RMNP are habituated to people and tolerate close observation. We observed free-ranging adult male moose as long as possible in an

attempt to record complete 24 h observation periods, 1 June-30 September 2003 and 2004. Individual moose were identified based on antler configuration, and an attempt was made to sample as many different moose as possible. Because individual moose were not marked, and an attempt to mark moose was unsuccessful, the same moose may have been sampled both years. Observer safety was assessed from the initial reaction of the moose to the observer and continued behavior over several hours before an observation shift began. A moose showing aggressive or annoyed behavior toward observers was not followed. We recorded locations of moose with hand-held global positioning systems (GPS) units. At night we used headlamps to record categorical behavior, but were unable to make detailed observations of feeding behavior (e.g., bite counts). Observations of different activities were recorded in journals, and we used hand-held voice recorders to document feeding behavior; observers were replaced every 8-10 h.

Activity Budgets

Activity patterns and time budgets were estimated by continuous time sampling over 24-h observation periods. Activities were categorized as resting, feeding, standing, extended movement, engaged in social interactions, and other (e.g., drinking, defecating, grooming). We recorded all major activities to the nearest minute. Extended movement was considered any movement lasting >5 min. We used only complete activity bouts lasting >15 min in our analyses of duration and number of feeding and resting bouts per day. Activity and resting bouts lasting ≤15 min were generally associated with disturbances caused by the observer or other animals. All activity data were used in estimating amount of time active per day and time budgets; data were grouped into biweekly periods.

Following Risenhoover (1986), we compared the amount of time spent active (feed-

ing, moving, social, other) during the day and night using the normalized day:night ratio (R) calculated by the equation:

$$R = \frac{D_a / D_t}{N_a / N_t}$$

where D_a is the number of daylight min active, D_t is the total of daylight min, N_a is the number of night min active, and N_t is the total number of night min. We estimated the length of day and night periods using sunset and sunrise data for Denver, Colorado obtained from the National Climatic Data Center, U.S. Department of Commerce, Washington, D.C.

Foraging Ecology

Feeding data were grouped into individual feeding bouts. We defined feeding bouts as any span of feeding ≥ 15 min. Feeding time within bouts was the sum of seconds spent biting, chewing, swallowing (but not ruminating), and moving between bites. We stopped voice recorders during non-feeding activities within bouts to calculate continuous feeding within bouts. Time was recorded at the end of each bout to estimate average bout length, and total feeding time within bouts was the proportion of the time spent continuously feeding within a given feeding bout.

We counted individual bites taken, and these were classified by plant species when possible. Bite rates (bites/min) were determined by continuous time sampling over the duration of the bout. Bite rate for each plant species was estimated during feeding periods, and mean bite rates were grouped according to species and bout.

During feeding periods, the sizes of all bites were recorded to estimate intake rates, and bites were classified as small (1-5 leaves), medium (5-10 leaves), or large (>10 leaves). After each observation, simulated moose bites were collected by clipping 10-20 samples/species in each of the 3 sizes. These samples

were bagged, oven-dried at 60 °C for 48 h, and weighed as described by Renecker and Hudson (1985). Bite size (g/bite) of each consumed plant species was estimated separately.

We calculated intake rate as the product of mean bite size and mean bite rate, both on an instantaneous and daily basis. Daily DMI (g/day) was the product of species-specific intake rates and foraging time per day for each species in the diet. Foraging time per day was the product of the average number of feeding periods per day and mean continuous feeding within bouts. Estimates of overall summer consumption were the product of daily DMI, number of days per period, and number of periods per summer.

We calculated digestible energy intake (DEI) by multiplying estimates of summer consumption of the principle forage (willow) by its dry matter digestibility (DMD) and gross energy (GE) estimates in the literature. The DMD of willow in RMNP during summer 2004 was 60.2% (Stumph 2005), and the GE estimate of willow was 20.38 kJ/g (Hjeljord et al. 1982). Metabolizable energy (ME) intake was assumed to be 88.6% of DEI (Schwartz et al. 1985).

Nutritional Carrying Capacity

We estimated nutritional K using data from the literature and from our feeding trials. First, our estimates of forage biomass was based solely on willow forage because 1) willow habitat was most used by all moose in all seasons in North Park, Colorado in 1991-1995 (Kufeld and Bowden 1996) and in summer in RMNP (Dungan 2007), and 2) 6 willow species comprise 91.3% of the summer diet in RMNP (June through mid-September) (Dungan and Wright 2005). Estimates of annual biomass production (269,974 kg), available dry matter (162,524 kg), and available protein (22,012 kg) of willow on the western side of RMNP were obtained from Stumph (2005). Because 100% use of forage is clearly not sustainable, we reduced total available biomass to reflect

sustainable utilization by moose. We based this reduction on the “allowable use criteria” recommended by Singer and Zeigenfuss (2002); we assumed that $\leq 21\%$ utilization of riparian willow by elk in RMNP would allow riparian willow communities to recover. Because more biomass is available during summer, we reduced total available biomass available to moose for foraging (R) by 75% (Frank and McNaughton 1992). This conservative reduction reduced our values of annual biomass production to 67,494 kg, available dry mass to 40,631 kg, and available protein to 5503 kg. The range supply (RS) of available nitrogen (N) was calculated by multiplying the available protein estimates by 0.16 (Robbins 2001). Available dry matter was calculated by multiplying estimates of annual biomass production by the digestibility coefficient (60.2%; Stumph 2005). The RS of digestible energy (DE) was calculated by multiplying estimates of available dry matter of willow by the GE content of willow (20.38 kJ/g; Hjeljord et al. 1982). Finally, the RS of ME was the product of DE \times 0.89 (Schwartz et al. 1985).

Next, we calculated energy and nitrogen requirements of moose from the literature. Unfortunately we were unable to weigh our study moose and summer weights of moose in

Colorado were also unavailable. Because most of our foraging data were recorded from adult bulls (5.5+ years), we used an estimate of the body mass of male Shiras moose from Lander, Wyoming during winter (344 kg; Hanna et al. 1989). Daily energy requirements for maintenance were calculated from this body mass using 1) activity budgets measured from our moose, and 2) the energy expenditure of 2 free-ranging, non-pregnant female moose weighing 320 ± 5 kg during July in central Alberta, Canada (Renecker and Hudson 1989a). The time spent per day in various activities during summer was multiplied by the energetic costs of those activities, and the costs summed over 24 h (Table 1). The nitrogen requirement for winter maintenance was estimated as $0.627 \text{ g/kg BW}^{0.75}/\text{d}$ (Schwartz et al. 1987b). Because no estimate of nitrogen requirement for summer maintenance exists, this estimate was increased 33% ($0.835 \text{ g/kg BW}^{0.75}/\text{d}$) to match the % increase of activity level during summer (VanBallenberghe and Miquelle 1990).

Using data on energy and nitrogen production at RMNP and energy and nitrogen requirements of moose, we estimated K for male moose on summer range in RMNP during the 2004 growing season with 3 different

Table 1. Calculations of daily energy requirements for a 344 kg moose during summer in Rocky Mountain National Park, Colorado.

Activity	Daily time spent per activity (hr)	Energy cost ^a per activity (kJ/kg BW ^{0.75} /hr)	Daily energy cost (kJ/kg BW ^{0.75} /day)
Feeding	8.91	39.7	353.7
Resting	4.53	26.9	121.9
Resting/Ruminating ^b	9.17	30.0	275.1
Moving	0.55	71.1	39.1
Standing	0.50	51.3	25.7
Social Interactions ^c	0.34	57.4	19.5
Total			835.0

^a Energy cost estimates are the average expenditure costs for various activities in May and July; taken from Renecker and Hudson (1989a).

^b Time spent resting/ruminating is based on 67% time spent resting (Risenhoover 1986).

^c Energy cost of social interaction was based on estimates of grooming (Renecker and Hudson 1989a).

models. The first model was based on estimates of DEI across the summer and the RS of DE. The second model was based on the RS of ME and the daily energy requirements of an adult bull moose. The third model was based on the RS of available N and daily N requirements of moose.

The estimate of K on summer range in RMNP was calculated in Model 1 by dividing the RS of DE by DEI during the summer, in Model 2 by dividing the RS of ME by the product of daily energy requirements multiplied by number of days of summer, and in Model 3 by dividing the RS of available N by the daily N requirements during summer. We assumed that summer was 106 days (1 June-15 September) based on observations from May-December, 2002-2004 (Dungan 2007).

Statistical Analyses

We compared biweekly differences in active time per day, number of feeding periods per day, duration of feeding and resting bouts, continuous feeding within feeding bouts, day:night ratios, species-specific bite sizes, species-specific bite rates, and rate of movement within feeding bouts using a two-way analysis of variance (ANOVA) (Sokal and Rohlf 1987), with time periods and years as the main effects. We compared differences in percent time engaged in different activities (time budgets) using a two-way parametric ANOVA on arcsine-transformed data to correct for non-normal distributions (Sokal and Rohlf 1987). Experimental units were complete 24-h observation periods for these analyses. Following Van Ballenberghe and Miquelle (1990), changes in the duration of feeding and resting bouts during the 24-h day were tested by dividing the day into eight 3-h periods and comparing means.

We used linear regression to separately analyze the relationship between mean temperature and the duration of feeding and resting bouts, and between movement and bite rates within feeding bouts. We used non-linear re-

gression to analyze relationships between bite sizes and bite rates. We compared differences in the duration of feeding bouts and mean temperatures within bouts using a one-way parametric ANOVA. For this analysis, we only used data from feeding bouts recorded during midday, and from late June-August, because of significant differences in feeding bout length during other periods. We obtained temperature data every 15 min from a mini-weather station located within the study area (Universal Transverse Mercator zone 13, Northing 4470423.01, Easting 427322.43, elevation 2719.10 m), and used those data to estimate temperature during resting and feeding bouts.

All pairwise differences were located using the Tukey HSD procedure. Differences were considered significant at $\alpha < 0.05$ and all statistics were performed using SAS 8.3 (SAS Institute Inc., Cary, North Carolina) statistical software. Results are reported as mean \pm standard deviation (SD).

RESULTS

Activity Budgets

Active time per day — We recorded 208 individual free-ranging male moose during summer 2003 and 2004; 55 individual males were identified based on antler configuration and photographs with 29 observed on multiple occasions. Direct observations resulted in 1456 h of data collected June-September, 2003 and 2004. Data for 37 complete 24-h observation periods were obtained from 17 individual adult males. Data on duration of activity and resting bouts were obtained from both complete and incomplete 24-h observation periods. Activity budgets did not differ between years ($F = 0.11$, $df = 1, 28$, $P > 0.05$); therefore, data were pooled across years for biweekly comparisons of activity. Daily activity fluctuated greatly across months ($F = 2.54$, $df = 5, 28$, $P = 0.05$) (Table 2).

Time budgets — Moose averaged 10.1 h/day active and 13.9 h/day inactive during sum-

Table 2. Mean ($\bar{X} \pm SD$) biweekly activity patterns of moose in Rocky Mountain National Park, Colorado, 16 June-15 September, 2003 and 2004. Letters indicate significant ($P \leq 0.05$) differences in activity patterns between periods. Day:night ratio refers to the time spent active during the day compared to night.

Period	<i>n</i>	Active hr/day	Feeding periods/day	Day:night ratio (:1)
June				
16-30	2	11.4 \pm 0.1 ^A	6.9 \pm 0.1 ^{AB}	1.23 \pm 0.13 ^{AB}
July				
Jan-15	3	10.3 \pm 0.8 ^{AB}	6.3 \pm 0.3 ^{AB}	0.79 \pm 0.14 ^B
16-31	6	10.8 \pm 0.2 ^A	7.3 \pm 0.5 ^B	1.27 \pm 0.44 ^{AB}
Aug				
Jan-15	10	9.0 \pm 1.1 ^B	6.9 \pm 0.6 ^B	0.98 \pm 0.21 ^B
16-31	4	8.9 \pm 0.9 ^B	7.2 \pm 0.5 ^B	0.89 \pm 0.14 ^B
Sept				
Jan-15	10	9.8 \pm 1.7 ^{AB}	5.5 \pm 0.7 ^A	1.64 \pm 0.46 ^A

mer and fall. Activities associated with feeding and resting constituted 94.0% of daily time budgets. Other activities included extended movement (2.3%), standing (2.1%), and social behavior (1.4%). The dominant social behavior was sparring (41.3%), followed by fraying and thrashing of trees (32.1%), smelling and following of females (15.2%), and pawing and urinating in pit holes (6.1%).

The percent time engaged in activities differed among biweekly time periods for feeding ($F = 3.29$, $df = 6, 28$, $P = 0.01$), extended movement ($F = 6.82$, $df = 6, 28$, $P = 0.0002$), and social behavior ($F = 6.24$, $df = 6, 28$, $P = 0.0003$). Feeding was lower in late September, larger extended movements occurred in late June and September, and social interaction was higher in mid-late September (Fig. 1). The average day:night ratio for time spent active (active day:active night) was 1.13:1. Average biweekly day:night ratios varied monthly ($F = 9.19$, $df = 5, 28$, $P < 0.0001$) peaking in late July and early September (Table 2).

Feeding and resting bouts — Moose engaged in more feeding bouts per day in late June-August than early September ($F = 11.97$, $df = 5, 28$, $P < 0.0001$) (Table 2). Duration of feeding bouts differed among bi-weekly time periods ($F = 4.98$, $df = 5, 270$, $P = 0.0002$) (Fig.

2a). The mean duration of feeding bouts was 79.4 \pm 29.9 min ($n = 277$, range = 19.3-277.7).

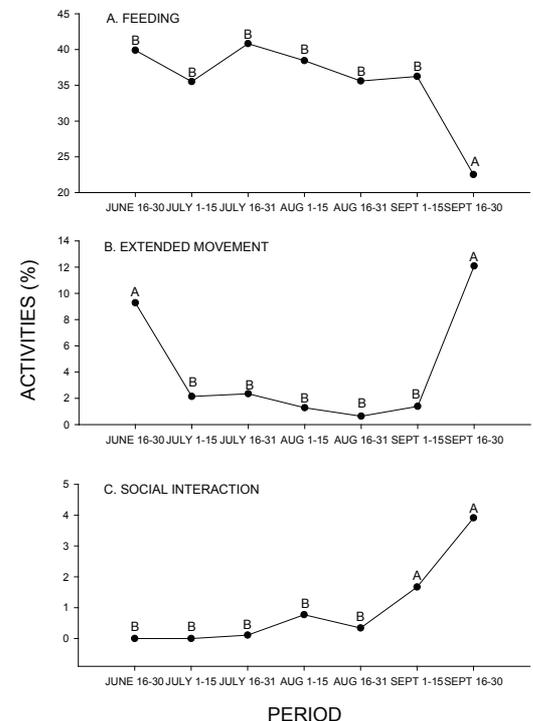


Fig. 1. Percentage of feeding (A), extended movement (B), and social interaction (C) activities of male moose during 2-week observation periods in Rocky Mountain National Park, Colorado, 16 June-30 September, 2003 and 2004. Letters indicate significant ($P \leq 0.05$) differences in activity levels between periods.

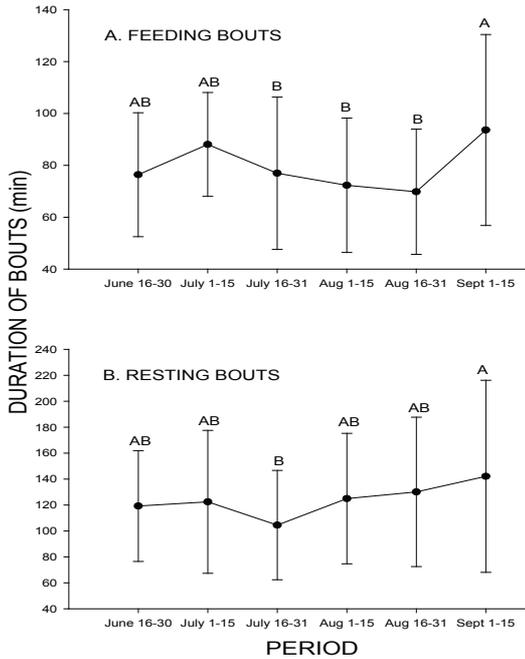


Fig. 2. Biweekly feeding (A) and resting (B) bouts of male moose in Rocky Mountain National Park, Colorado, 16 June-15 September, 2003 and 2004. Vertical bars indicate standard deviation (SD), and letters indicate significant ($P \leq 0.05$) differences in bout duration between periods.

Continuous feeding within bouts also differed ($F = 4.62$, $df = 5$, 212 , $P = 0.0005$) among bi-weekly periods; it was longest in early July (73.7 ± 29.7 min, $n = 19$) and early September (86.2 ± 32.4 min, $n = 70$), and lowest in late July (67.2 ± 26.3 min, $n = 66$). Continuous feeding within bouts averaged 12.2 min (range = 4.0-27.8) less than the mean bout length, with the greatest difference occurring in early September (27.8 min). The duration of resting bouts was also different among bi-weekly time periods ($F = 3.93$, $df = 5$, 275 , $P = 0.002$) (Fig. 2b); the mean was 125.9 ± 58.6 min ($n = 282$, range = 19.1-410.3).

The duration of feeding ($F = 3.61$, $df = 7$, 198 , $P = 0.0011$) and resting ($F = 5.49$, $df = 7$, 197 , $P < 0.0001$) bouts differed across the day. Feeding bout duration was longer around dawn and shortly after dusk than at midday and night; conversely, the resting bout dura-

tion was shortest those same periods (Fig. 3). The duration of feeding bouts declined with increasing mean temperature over 24-h period ($r^2 = 0.032$, $P = 0.01$), and between dawn and dusk ($r^2 = 0.21$, $P < 0.001$) (Fig. 4); length of resting bouts was not related to daily temperature ($r^2 < 0.001$, $P = 0.86$). During midday in June-August moose fed for shorter periods when temperatures were $>20^\circ\text{C}$ ($F = 28.74$, $df = 1$, 111 , $P < 0.0001$).

Foraging Ecology

Bite size, bite rate, and search effort –

Bite size differed among plant species consumed ($F = 22.77$, $df = 13$, 461 , $P < 0.0001$) and 2-week periods ($F = 7.56$, $df = 5$, 461 , $P < 0.0001$), but not among years ($F = 1.27$, $df = 1$, 461 , $P = 0.26$). Moose took the largest bites from quaking aspen (2.7 ± 0.1 g/bite) in early July; this was a result of stripping bark rather than solely cropping leaves. During summer the largest average bite size was taken from western dock (2.5 ± 0.2 g/bite), and the largest bite size of a species dominant in the diet was drummond willow (1.6 ± 0.4 g/bite) (Table 3). The smallest average bite size was from wolf willow (0.2 ± 0.02 g/bite) in early July. The mean size of simulated moose bites

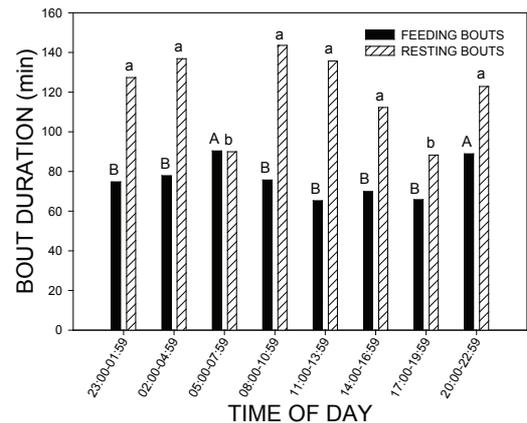


Fig. 3. Mean duration of activity and resting bouts in 3-h periods during diel observations of male moose in Rocky Mountain National Park, Colorado, 16 June-15 September, 2003 and 2004. Letters indicate significant ($P \leq 0.05$) differences in the duration of bouts between periods.

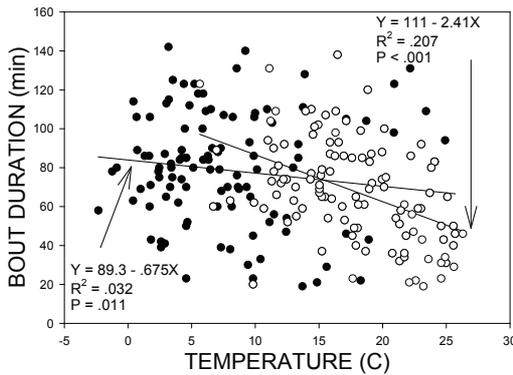


Fig. 4. The relationship between the duration of feeding bouts of male moose and temperature in Rocky Mountain National Park, Colorado, 16 June-31 August, 2003 and 2004. Filled circles represent data collected during the 24-h day, and open circles between dawn and dusk only.

(all species) increased from 1.1 ± 0.6 g/bite in late June, peaked at 1.4 ± 0.2 g/bite in early August, and declined to 0.9 ± 0.1 g/bite in early September. The mean size of a moose bite during summer was 1.1 ± 0.2 g/bite.

As a mechanical consequence of consuming different bite sizes, bite rates declined curvilinearly with increasing bite size ($r^2 = 0.94$, $P < 0.0001$) (Fig. 5). Bite rate differed among plant species ($F = 6.85$, $df = 13, 461$, $P < 0.0001$) (Table 3) and periods ($F = 16.75$, $df = 5, 461$, $P < 0.0001$), but did not differ between years ($F = 0.59$, $df = 1, 461$, $P = 0.44$). We recorded the highest bite rates for wolf willow (21.5 ± 2.9 bites/min) in early August, and the lowest for quaking aspen (6.3 ± 3.4 bites/min) in late July.

The rate of movement (search effort) during feeding bouts differed among periods ($F = 2.79$, $df = 5, 145$, $P = 0.01$) and between years ($F = 14.21$, $df = 1, 145$, $P = 0.0002$). We measured the highest average rates of movement in late June (2.5 ± 1.7 steps/min) and late August (2.4 ± 1.0 steps/min), and the lowest in late July (1.9 ± 0.9 steps/min). The average rate of movement during feeding bouts was higher in 2003 (2.3 ± 1.5 steps/min) than 2004 (1.6 ± 0.8 steps/min). Rate of movement was not related to bite rate during

feeding bouts ($r^2 = 0.04$, $P = 0.44$).

Dry matter intake—Daily DMI of male moose varied throughout the summer and autumn. The estimated mean daily consumption showed a steady increase in early summer peaking at 10,133 g/d (126.8 g/kg $BW^{0.75}$) in early August, followed by a sharp decline to a low of 5,522 g/d in early September (Fig. 6). The highest estimated intake rate (22.3 g/min) was recorded in early August; the low was 10.2 g/min in late June. Intake rates of willow (all species) increased from a season low of 11.2 g/min in late June to a peak of 18.7 g/min in early August, and declined to 11.7 g/min in early September. Species-specific intake rates during summer were highest for western dock and drummond willow, and lowest for bog birch (Table 3). Dry matter consumption was estimated in 2-week intervals from 1 June-15 September (106 days) with total summer consumption by male moose estimated at 822.8 kg.

Daily DEI increased in early summer peaking at 1555 kJ/kg $BW^{0.75}$ ($124,257$ kJ/d) in early August, and declined to a season low of 847 kJ/kg $BW^{0.75}$ ($67,714$ kJ/d) in early September. Daily DEI was estimated as 1191 kJ/kg $BW^{0.75}$ ($95,182$ kJ/d), and overall summer DEI was estimated at 1008.9×10^4 kJ. Daily ME intake was estimated as 1055 kJ/kg $BW^{0.75}$ /d.

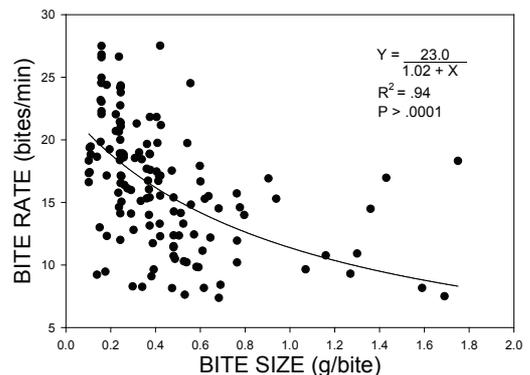


Fig. 5. The relationship between bite size and bite rate of moose in Rocky Mountain National Park, Colorado, 16 June-15 September, 2003 and 2004.

Table 3. Bite size, bite rate, and intake rate (i.e., the product of bite size and bite rate) by moose during summer 2003-2004 in Rocky Mountain Park, Colorado. Different letters denote significant differences ($P \leq 0.05$) among bite rates.

Species	Bite size (g/bite)			Bite rate (bites/min)			Harvesting rate (g/min) ^a
	n	x	SD	n	x	SD	
arrow-leaved groundsel (<i>Senecio triangularis</i>)	3	1.56	0.03	3	12.16 ^{AB}	1.86	18.96
bog birch (<i>Betula glandulosa</i>)	11	0.54	0.02	15	16.39 ^{AB}	4.50	8.84
drummond willow (<i>Salix drummondiana</i>)	28	1.56	0.35	36	15.38 ^B	4.88	23.98
geyer willow (<i>Salix geeyeriana</i>)	52	1.08	0.12	128	14.29 ^B	4.36	15.43
grasses	20	0.66	0.16	24	16.75 ^{AB}	7.46	11.04
mountain alder (<i>Alnus incana</i>)	23	1.30	0.23	40	15.70 ^B	4.05	20.42
mountain willow (<i>Salix monticola</i>)	61	1.32	0.26	77	14.88 ^B	4.81	19.64
plane-leaf willow (<i>Salix planifolia</i>)	45	0.60	0.05	119	18.70 ^A	4.81	11.22
western dock (<i>Rumex aquaticus</i>)	8	2.48	0.19	10	14.93 ^{AB}	7.39	37.02
thistle (<i>Cirsium spp.</i>)	2	1.28	0.03	2	15.24 ^{AB}	0.66	19.50
trembling aspen (<i>Populus tremuloides</i>)	6	1.80	0.31	7	12.29 ^B	4.18	22.12
whiplash willow (<i>Salix lasiandra</i>)	6	1.38	0.22	8	13.97 ^{AB}	6.52	19.26
wolf willow (<i>Salix wolfi</i>)	3	0.64	0.04	8	20.51 ^A	2.35	13.12
yellow water-lily (<i>Nuphar lutea ssp. Polypetalum</i>)	3	2.18	0.17	3	10.72 ^{AB}	1.96	23.36

^aIntake rate is the product of mean bite size and mean bite rate.

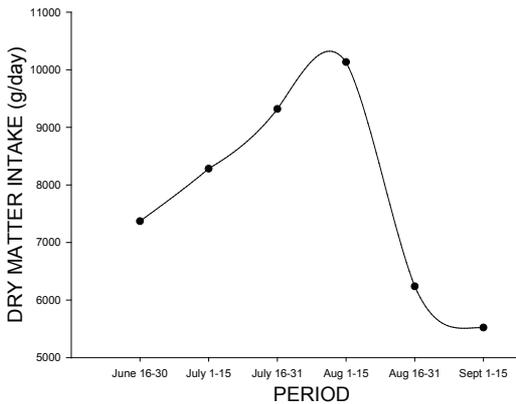


Fig. 6. Dry matter intake (g/day) of free-ranging male moose in Rocky Mountain National Park, Colorado, 16 June-15 September, 2003 and 2004. Estimates are based on bite-count techniques.

Nutritional Carrying Capacity

The total RS of willow habitat represented 3310.4×10^6 kJ of DE, 2946.2×10^6 kJ of ME, and 3521.9 kg nitrogen during summer 2004. The estimated available biomass that would provide sustainable moose foraging (i.e., available dry matter reduced by 75%) was 67,494 kg (dry weight). The estimates of K with Model 1 and 2 were similar; Model 1 estimated 82 moose or 0.21 moose/km² and Model 2 estimated 83 moose and 0.21 moose/km². Model 3 predicted a K of 125 moose and 0.32 moose/km², estimates 34% higher than those of Models 1 and 2.

DISCUSSION

Our observations of summer activity patterns and foraging ecology of moose in RMNP at the southernmost extent of their range fills a key gap in the understanding of environmental interactions between moose and willow habitats. It complements and provides a novel ecological comparison with the extensive research of activity patterns (Risenhoover 1986, Renecker and Hudson 1989b, Bevins et al. 1990, VanBallenberghe and Miquelle 1990) and foraging ecology (Miquelle and Jordan 1979, Schwartz et al. 1984, Renecker and Hudson 1985, Renecker and Hudson 1986b) of moose in their northern

range in North America.

Activity Budgets

The activity of male moose in RMNP fluctuated during summer through fall, and these fluctuations are most likely attributable to changes in behavior preceding the breeding season. Moose were most active in early summer, feeding for 82% of the 10 h/d they spent active. Similarly, free-ranging moose in Denali National Park (DNP), Alaska spent 13 h/d active during early summer, feeding for about 75% of their active time (VanBallenberghe and Miquelle 1990). As breeding season approached in early fall, activity level of moose in RMNP declined to <9 h/d. Activity levels increased with the onset of the breeding season in fall, but the proportion of time spent feeding declined to 52% of active time. Moose spent more time moving and in social activities related to breeding; sparring and thrashing trees began around 1 September with smelling and following females towards the end of September. A reduction in feeding and increase in social behavior during breeding season was also observed in Alberta, Canada (Best et al. 1978, Renecker and Hudson 1989b). Schwartz et al. (1984) noted complete fasting by males as long as 18 days during the breeding season.

Little is known about the nocturnal activity of moose (Klassen and Rea 2008), and to the best of our knowledge this is the first study to record activity patterns of free-ranging moose for extended periods at night (between dusk and dawn). Although moose were 13% more active during day than night, these observations were influenced by early season movements spent searching for suitable forage and late season mating behavior, both done mostly during the day. During July and August moose were up to 20% more active at night than during the day (Table 2). Likewise, Renecker and Hudson (1989b) found penned moose in Alberta, Canada were more active at night during spring and summer than in fall

and winter. Feeding and resting/ruminating dominated nocturnal activity of our moose throughout summer, and extended movement (>5 min) was rarely observed at night. Predation of moose within RMNP is considered rare, and hunting is not allowed within RMNP, thus predator avoidance at night may be less influential and contribute to low movement at night. Ericsson and Wallin (1996) found increased diurnal movement during hunting season in northern Sweden.

Although moose had fewer feeding bouts/d as fall breeding approached (Table 2), mean feeding bout duration in early September was longer than in summer because moose spent more time socializing during feeding bouts; continuous feeding within activity bouts was also highest at that time resulting in similar time spent foraging during summer and early fall. Renecker and Hudson (1989b) found that the longest foraging bouts of captive moose occurred in spring and fall, and the number of activity bouts/d did not vary between seasons. The number of activity bouts/d varied between and within seasons, as also reported by Bevins et al. (1990), VanBallenberghe and Miquelle (1990), and MacCracken et al. (1997). The variation among studies may be attributed to the differences in behavior of free-ranging and captive moose. Free-ranging moose most likely endure more environmental constraints than captive moose. The average number of feeding bouts/d was similar to that measured in Michigan (Miquelle and Jordan 1979), Alberta, Canada (Bevins et al. 1990), and DNP, Alaska (VanBallenberghe and Miquelle 1990).

The length of feeding bouts during the day declined as ambient temperature increased (Fig. 4), similar to that reported for moose in other studies (Ackerman 1987, Bevins et al. 1990, VanBallenberghe and Miquelle 1990). Thermal stress in moose begins at 14-20°C, and when temperatures exceed 20°C, metabolic rates of moose increase at a rate of 0.7 kJ/kg BW^{0.75}/h/°C (Renecker and Hudson 1986a).

Temperatures regularly rose above 20°C during the afternoon in mid-June to mid-August in RMNP. When temperature was >20°C, the length of foraging bouts declined, and moose were rarely observed feeding for extended periods during midday, and typically bedded in shade or water. However, they did not shift to nocturnal feeding suggesting that temperature in RMNP was not high enough to cause major behavioral change in foraging activity. Kelsall and Telfer (1974) suggested that areas with prolonged temperature >27°C are unsuitable for moose because of thermal stress, and temperature rarely reached that level.

Peak feeding times for moose were around dawn and dusk (Fig. 3) as indicated in previous studies (Cederlund et al. 1989, Renecker and Hudson 1989b, MacCracken et al. 1997); the timing of feeding shifted with photoperiod. However, summer studies in Alaska where days are longer indicated less synchrony of feeding at dawn and dusk (Bevins et al. 1990, VanBallenberghe and Miquelle 1990). Best et al. (1978) concluded that moose activity in Alberta, Canada was controlled by light and triggered daily by sunrise and sunset; our data are supportive of this. If activity is triggered by photoperiod, continuous daylight during Alaskan summers would lead to less synchrony of moose activity. It follows that studies at different latitudes and seasons should not necessarily yield similar results. We estimated the average daily energy expenditure of male moose in summer at 835 kJ/kg BW^{0.75}/d, similar to the mean for 2 free-ranging moose cows in May and July (890 kJ/kg BW^{0.75}/d; Renecker and Hudson 1989a). Energy expenditure during summer is considerably higher than in winter (Schwartz et al. 1987a, Schwartz et al. 1988a, Renecker and Hudson 1989a), most likely because of increased metabolic rate (Renecker and Hudson 1986a), increased activity (Renecker and Hudson 1989b, VanBallenberghe and Miquelle 1990), and higher ambient temperature (Renecker and Hudson 1989a).

Foraging Behavior

Moose had the highest harvesting rates on plants from which they could obtain the largest bites. Bites >2 g were measured for 2 aquatic plants, western dock and Rocky Mountain cow-lily. The harvest rate of willow averaged 17.1 g/min, with the largest bite size and fastest harvest on drummond willow and the smallest bite and slowest harvest on wolf willow. Because larger bites require more time to chew (Risenhoover 1989), bite rates were lowest on the plant species from which moose took the largest bites. Bite size, bite rate, and harvest rate of willow were similar to those reported by Renecker and Hudson (1986b) for cow moose in summer in Alberta, Canada, and moose in DNP (Van Ballenberghe, unpublished data). The mean bite size increased early in summer, peaked in early August at the height of the growing season, and declined in early September with the senescence of available forage.

Daily DMI varied in the study, slowly increasing from May to August, followed by a sharp decline in fall (Fig. 6). Consumption likely mirrored the changes in willow biomass that peaked in late summer (Stumph 2005). Decreases in DMI in fall are usually associated with the onset of breeding. Peak DMI in early August and DMI estimates were similar to those reported for moose in Alaska and Alberta, Canada (Schwartz et al. 1984, Renecker and Hudson 1985, Miquelle and Jordan 1979), and predictions from a simulation model (Hubbert 1987). Estimates of daily ME intake across the summer were well above the estimated ME requirements for free ranging moose (584.7 kJ/kg BW^{0.75}/d; Renecker and Hudson 1985), indicating that moose were able to obtain adequate energy for maintenance and replenishing fat reserves. Peak DEI did not coincide with peak nutritional content of willow. Crude protein of willow peaked around late June in 2003, and mid-June in 2004 for all species (Stumph 2005); however, intake rates of willow peaked in early August suggesting

that the available biomass of willow is likely more important than its protein content.

Carrying Capacity Estimates

The estimate of nutritional K from the nitrogen-based model (3) was about 34% higher than those from the energy-based models (1 and 2). We suspect that Model 3 overestimated K and attribute the larger estimate to our assumptions and use of the 33% multiplier to estimate nitrogen requirements. The same estimates were more similar for elk during winter in RMNP (Hobbs et al. 1982) however, estimates of energy requirements are less complex in winter than summer.

Because >90% of the summer and fall diet of moose in RMNP is willow (Dungan and Wright 2005), modeling carrying capacity was much simpler than in situations where herbivores consume a wide range of plants that vary substantially in nutritional quality and concentrations of plant secondary metabolites (Hobbs and Swift 1985, Beck et al. 2006). Although moose consumed 6 species of willow that differ somewhat in nutritional quality (0.99-1.43% available N, 51.7-59.9% available dry matter; Stumph 2005), and a minor proportion of 14 other species or categories of plants (Dungan and Wright 2005), we believe that basing estimates of K on total willow biomass, average willow quality, and diet selection, activity patterns, and intake rates of moose provided a reasonable estimate of the number of moose that can be supported by the riparian communities in RMNP in summer. However, direct inference to other locations or seasons should be cautious.

Because 100% use of forage by ungulates in most ecosystems reduces plant productivity and is not sustainable (McInnes et al. 1992, Pastor et al. 1993), and ungulates are not capable of consuming forage at that level, researchers have reduced estimates of forage availability based on snow depth (Potvin and Huot 1983, Stephenson et al. 2006), diet choice (Wallmo et al. 1977, Hobbs et al. 1982,

Stephenson et al. 2006), and habitat selection (Beck et al. 2006). We conservatively reduced available browse estimates by 75% (25% sustainable use), although some studies have considered consumption rates of 42-50% sustainable for shrub communities (Wolfe et al. 1983, Bergstrom and Danell 1987, Singer et al. 1994). The reduction of available biomass greatly reduced the estimates of K for moose on the western side of RMNP, and higher consumption rates of riparian willow communities may indeed be sustainable.

MANAGEMENT IMPLICATIONS

Willow communities in the portion of RMNP west of the Continental Divide have experienced degradation over the last 100 years. Two historic influences were 1) water diversions from the upper Colorado River to eastern Colorado put in place prior to establishment of RMNP, and 2) intensive trapping of a still-depleted beaver population in the 19th and early 20th centuries (Hess 1993). More recently drought, climate change, and an expanding elk population have likely added stress to native plant communities, particularly riparian willow habitat. This study has not only provided valuable information to evaluate the moose population and its sustainability in the western part of RMNP, but it also aids in addressing the larger issue of willow communities. Our study estimated that 82-125 moose could be sustained in this 391 km² area west of the Continental Divide, which is 30-72% more than the 37-59 moose estimated as resident in summer, 2003-2004 (Dungan 2007); thus, moose at present pose no measurable ecological threat in the study area. Importantly, our data should be useful to estimate K for moose in willow communities on the east of the Continental Divide that are more degraded and heavily used by elk (Singer and Zeigenfuss 2002), should moose ever disperse to this area of RMNP.

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