

SEASONAL HABITAT USE CHARACTERISTICS OF MOOSE IN SOUTH-CENTRAL MONTANA

Fred Van Dyke¹, Brenda L. Probert² and Grant M. Van Beek¹

¹Department of Biology, Northwestern College, Ornage City, IA 51041; ²Department of Wildlife Ecology, University of New Hampshire, Durham, NH 03824.

ABSTRACT: We examined habitat use in home ranges and seasonal core use areas by 13 radio-collared Shiras moose (*Alces alces shirasi*) in south-central Montana from 9 January 1989 to 16 August 1993. Moose selected for aspen (*Populus tremuloides*) and against lodgepole (*Pinus contorta*) forests in every season, and selected for shrub-dominated wetlands communities in winter and spring. Core foraging areas differed in plant community characteristics but were similar in coverage and volume of shrubs and graminoids, with shrubs being the dominant vegetational component. Core areas also differed in nutritional values of browse, with highest total energy associated with core areas in alpine vegetation. Moose in this population probably would benefit from intensive management of heavily used areas and creation of aspen and shrub habitats through prescribed burning of aspen and selective removal of lodgepole pine. Sites with >42% shrub coverage and >3600 m³/ha of shrub volume probably would be used as core foraging areas.

ALCES VOL. 31 (1995) pp.15-26

Habitat quality can be defined as the ability of a range to produce or sustain desirable population characteristics (Risenhoover 1989). A first approximation to understanding habitat quality begins with an assessment of habitat use, and can be refined by examining differences between seasons and individuals. Food quantity and quality change seasonally concomitant with metabolic needs of moose (Schwartz *et al.* 1984, Regelin *et al.* 1985). Such variations are important determinants of how animals allot time and energy for various activities (Belovsky and Jordan 1978, Risenhoover 1986, Van Ballenberghe and Miquelle 1990). As a result of such changes, moose habitat use also can be expected to change seasonally (Cederlund and Okarma 1988). Seasonal variation in moose habitat use has been studied in boreal forest moose in Minnesota (Peek *et al.* 1976), Canada (Hauge and Keith 1981, Mytton and Keith 1981), and Sweden (Cederlund and Okarma 1988), and in Shiras moose of the western United States (Pierce and Peek 1984), but few studies have assessed habitat use on an annual basis for >3 years.

Moose show adaptability to a variety of available forage, and especially of early successional or post-disturbance shrubs (Franzmann 1978). Their traditionally non-uniform use and slow movement through their home areas (Van Ballenberghe and Peek 1971, Garton *et al.* 1985) is probably due to the disproportionately high use moose make of small, core foraging areas, where abundance of shrub vegetation is assumed to be high. Van Ballenberghe and Peek (1971) described moose home ranges as a series of high use areas connected by wanderings. Cederlund and Okarma (1988) hypothesized that moose home areas actually may be comprised of closely located feeding sites on < a few ha that could be used for a few days up to several weeks. Such core areas are believed to support higher densities, volumes, and nutritional quality of early successional shrub vegetation, but the precise habitat characteristics of such core areas have not been well documented.

We studied seasonal variation in habitat and core area use in a moose population inhabiting the Beartooth Mountains of south-

central Montana. Home range analysis of moose in this population (Van Dyke *et al.* 1996) indicated intense use of relatively small portions of home areas (core areas). Because home range use suggested that such core areas were of great importance to moose, we focused our sampling and analysis effort on such areas, believing that greater insight into moose habitat selection could be gained from a more intensive examination of the vegetation characteristics of these core foraging areas.

Our objectives were to provide a more precise description of both moose habitat use and moose core area characteristics to aid in the development of a comprehensive moose management plan for the Beartooth District of the Custer National Forest. Our specific goals were to test the null hypotheses that: (1) habitat use would not be different from expected (available), or different between seasons or sexes; (2) elevational use would not differ between seasons or sexes; and (3) individual core areas would not differ from each other in plant coverage or nutritional characteristics. We did not, however, compare core area vegetation with the study area

as a whole.

STUDY AREA

The study was conducted on the Custer National Forest in the Fiddler and Fishtail Creek drainages, tributaries of the Stillwater River in south-central Montana. Moose in this area use elevations between 1500 m and 2800 m and terrain characterized by gently rising east-facing slopes of the Fishtail and Stillwater Plateaus in Carbon and Stillwater Counties, MT. Ratios of collared to uncollared moose observed on repeated winter survey flights indicated that the area contained approximately 60-70 individuals within approximately 125 km², or approximately 1 moose/2 km² (S. T. Stewart, MDFWP, pers. commun.). Observations from the same flights suggested that the population was female-dominated at a ratio of approximately 1 male:3 females.

Long, cold winters and short, cool summers typify climate. Snow began to accumulate by November and usually remained until May. During the main period of the study (1989-91), mean January and July temperatures at the Mystic Lake, MT reporting sta-

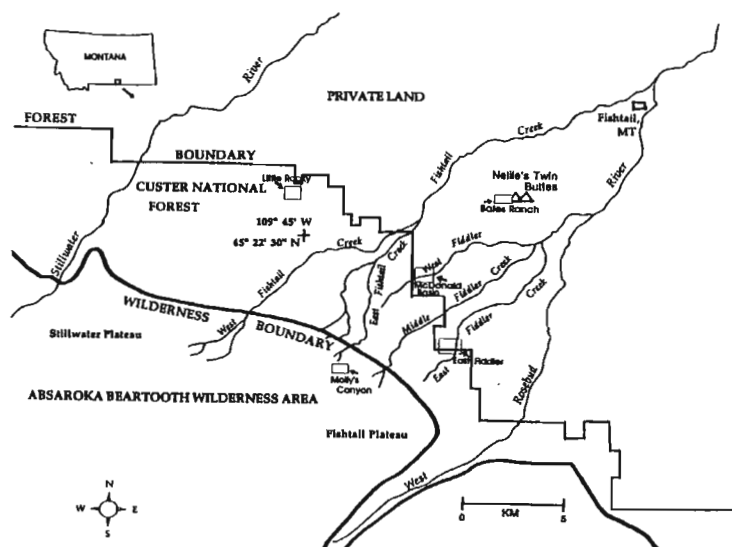


Fig. 1. Study area of the fiddler-Fishtail moose population in south-central Montana, 1989-92. Enclosed areas (Bates Ranch, East Fiddler, Little Rocky, McDonald Basin, and Molly's Canyon) represent approximate locations, boundaries, and sizes of 5 core foraging areas of 5 female moose.

tion near the center of the study area (elevation 1997 m) were -3°C and 18°C , respectively. Annual temperatures ranged from -46°C to 38°C . Annual rainfall averaged 56.8 cm and annual snowfall averaged 386 cm (U. S. Department of Commerce 1992).

Upland areas usually were dominated by immature stands of lodgepole pine to the base of the plateaus, with less frequent occurrence of Douglas fir (*Pseudotsuga menziesii*) on steeper north slopes of lower elevation ridges. Subalpine forests of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) occurred on mesic sites at higher elevations. On mesic sites at low and intermediate elevations, stands of quaking aspen were common, and often adjacent to shrub-dominated wetland communities characterized by mountain alder (*Alnus incana*), willow (mainly *Salix planifolia* and *S. discolor*), and red osier dogwood (*Cornus stolonifera*). On drier sites at lower elevations stands of Ponderosa pine (*Pinus ponderosa*) often occurred adjacent to upland shrub communities dominated by chokecherry (*Prunus virginiana*), ninebark (*Physocarpus malvaceus*), and wild plum (*Prunus americana*).

METHODS

Assessment of Habitat Utilization

Thirteen moose (3 males, 10 females) were captured by helicopter darting (Nielson and Shaw 1967) during December 1988 and 1990 and January 1991 and fitted with radio neck-collars (SB2 transmitter and Lonner module collar, AVM Instrument Co., 2356 Research Drive, Livermore, CA 94550 and Mod 500 transmitters, Telonics, 932 East Impala Avenue, Mesa, AZ 85204). Moose were located 730 times from 9 January 1989 to 6 March 1992 and subsequently from 18 June 1993 to 16 August 1993. Moose were located by fixed-wing aircraft or by close ground triangulation between 0500 and 2200 hours. Non-visual aerial locations were test-

ed for accuracy by placement of a transmitter at an unknown location. Average error was 143 m. Aerial locations were recorded after visual observation or after repeated circlings permitted the signal to be confined within a circle of 300 m diameter using a directional antenna mounted beneath the aircraft. Ground locations were recorded after visual observation, close triangulation (triangulation from >2 points <100 m from the moose), or ability to hear the signal on the receiver without the antenna or cable. Field tests prior to the start of the study demonstrated that the latter occurred only at distances <50 m.

Locations were recorded in Universal Transverse Mercator coordinates to the nearest 100 m. Time, date, individual, elevation, and habitat type were noted at each location. Locations were grouped by seasons defined as winter (December-February), spring (March-May), summer (June-August), and autumn (September-November). Minimum convex polygon (Hayne 1949) estimates of home range size and boundaries using 95% innermost locations were calculated using the HOME RANGE animal location analysis program (Ackerman *et al.* 1990). HOME RANGE then identified core use areas by comparing actual home range use to a uniform utilization distribution (Samuel *et al.* 1985).

Analysis of Elevation and Habitat Use

Seasonal elevational use by moose was evaluated through an AOV in which elevation was treated as the dependent variable and sex and season as independent variables (main effects) using GLM procedures in SAS for unbalanced designs (SAS Institute Inc. 1989:898-899). Where significant differences were detected in main effects, differences between individual means were tested using Fisher's Least Significant Differences (LSD) procedure to control the family-wise type I error rate.

Habitats at moose locations and random

points originally were classified according to Pfister *et al.* (1977) and Mueggler and Stewart (1980), but later were simplified to aspen, lodgepole, shrub-dominated wetland, other coniferous forest (Ponderosa pine, Douglas fir, and subalpine forest), or other non-forest habitat. Relationship of habitat use to season, sex, and random availability was evaluated through an SAS categorical data modeling procedure, CATMOD (SAS Institute Inc., 1989:405-517). Individual hypotheses related to particular season and sex comparisons were evaluated through specific CONTRAST statements in the analysis program (SAS Institute Inc. 1989:419-420). Random availability of habitat was estimated from the distribution of habitat types found at 160 points, selected randomly along principal UTM grid lines which passed through previously determined moose home ranges. Habitat types of random points were determined from on-the-ground site inspection and values of physical and vegetative variables measured at the site. Where significant overall differences were detected, comparisons between use and availability in individual habitat categories were evaluated by constructing simultaneous confidence intervals of habitat use from Bonferroni Z-tests (Neu *et al.* 1974, Marcum and Loftsgaarden 1980).

Core areas of 5 female moose followed for >2 years were designated for more intensive study of plant characteristics after completion of preliminary home range analysis in 1991. These areas were identified as East Fiddler (EF), McDonald Basin (MB), Little Rocky (LR), Bates Ranch (BR), and Molly's Canyon (MC) (Fig. 1). All five core areas received heavy use in spring and early summer (March-June). Some received extended use in other seasons. This included extensive summer and autumn use in EF and MC, autumn and winter use in MB, and autumn use in BR. Four to 9 different 20.1 X 20.1 m (404 m²) macroplots were established at >100 m intervals in the most intensively

foraged portions of each core area (determined from moose observations and locations) in June and July 1991 and 1993, a period when all moose were still using or had just completed using all of the above core areas. The number of macroplots established was contingent upon the size and configuration of the core area as determined by actual radio locations of the individual moose, and was designed to maximize coverage of those portions of the core area where feeding actually occurred.

Six 20.1 m X 66 cm transects were established within each macroplot along the macroplot baseline at intervals determined from a random number table. Plant coverage and height, by species, were determined in 5 25.4 X 50.8 cm microplots sampled at 3.7 m intervals along each transect. Coverage of plants was determined by visual estimations within a visually calibrated microplot frame. Coverage, frequency, and volume of each plant species and category (shrubs, forbs, and graminoids) were calculated using the USFS ECODATA vegetation analysis program. Though invoked less frequently than estimates of plant biomass (e. g. kg/ha), plant volume measurements have been used in many field studies to quantify vegetation and habitat characteristics (e. g. Mills *et al.* 1991, Johnson 1992), and as an assessment of plant biomass and productivity (Kittredge 1945, Chew and Chew 1965, Whittaker and Woodwell 1968, Ludwig *et al.* 1975, Schreuder and Williams 1995). We found volume measurements to be a more efficient and more appropriate method for quantifying vegetation data in moose core use areas compared to biomass measurements due to the coverage, densities, and growth forms of core area vegetation, particularly in regard to shrubs. Data from 1991 and 1993 were combined after analysis demonstrated that year had no significant effect on the above variables.

Because not all vegetation represented

palatable browse, further analysis of plant nutrition in core areas was conducted in 1993 to determine actual nutritional value of browse found in core areas. New growth leaders of woody plants in 8 randomly selected transects in each core area (<2/macroplot) were clipped and bagged. Recurrent bad weather on sampling days in the LR core area forced us to reduce sample size in this core area from 8 to 6. No samples were taken from the MB core area because of the landowner's request not to clip and remove vegetation. Clipped samples were taken to the Analytical Chemistry Laboratory, Montana State University, Bozeman, to determine dry weight levels of moisture (%), crude dietary protein (%), gross energy (kcal/kg), Ca, K, Mg, Na, and P. Standard analytical techniques were used following procedures described by the A. O. A. C. (1965).

Statistical Analysis of Core Area Vegetation

Differences between plant characteristics in core areas were evaluated by an AOV which treated measurements of plant coverage and volume as dependent variables and site as the classification variable (main effect). A similar analysis was conducted for nutritional variables. Where significant differences occurred among sites, individual

differences were compared using Fisher's Least Significant Differences (LSD) procedure to control the family-wise type I error rate.

RESULTS

Elevation and Habitat Use

Mean seasonal elevations inhabited by moose ranged from 1781 m in spring to 1949 m in autumn (Table 1). Both sex and season had significant effects on elevational use ($P < 0.01$, both effects). Summer and autumn elevations were higher than winter and spring ($P < 0.01$). Males inhabited lower elevations than females ($P < 0.01$).

Concurrent with changes in elevational use, moose of both sexes selected habitats in a manner different from random in all seasons ($P < 0.01$, both sexes). Both season and sex had significant influence on habitat selection ($P < 0.01$, both effects). In individual seasons, sex was a significant influence in summer and autumn, but not in winter ($P < 0.01$ and $P = 0.11$, respectively). Data were insufficient for male moose in some habitat categories to evaluate sexual differences in spring. All seasons differed from each other in distributions of utilized habitats ($P < 0.01$, all comparisons).

Moose selected for aspen and against lodgepole in every season, and for shrub-

Table 1. Average seasonal elevations (m) of radio-collared moose in Fiddler and Fishtail Creek drainages, south-central MT, 1989-93. SE/N (numbers of relocations) in parentheses.

Season	Elevation (m)		
	Males ^a	Females	All moose
Winter ^b	1706 (12/37)	1835 (25/118)	1807 (16/155)
Spring ^b	1738 (20/30)	1789 (9/153)	1781 (9/183)
Summer	1870 (14/63)	1937 (21/168)	1914 (16/231)
Autumn	1866 (22/43)	1980 (28/118)	1949 (21/161)

^a Different from females, all seasons. $P < 0.01$.

^b Different from summer and autumn, both sexes. $P < 0.01$.

dominated wetlands communities in winter and spring (Table 2, $P < 0.01$, all cases). Selection for shrub-dominated wetlands communities approached significance in autumn ($P = 0.06$), but moose showed no selection for this habitat type in summer. Other non-forest habitat was selected against in winter ($P = 0.02$).

Selection tendencies for aspen and against lodgepole communities were the same in males and females (Table 2, $P < 0.01$, both cases), but males selected aspen more and lodgepole less than females ($P < 0.01$, both cases). Females showed significant selection for shrub-dominated wetlands communities ($P < 0.01$). Male use of this habitat was similar and approached significance ($P = 0.06$). Males showed selection against other non-forest habitats ($P < 0.01$), but females used it in proportion to availability.

Core Area Vegetation Characteristics

Site location had significant overall effects on vegetation coverage, volume, and nutritional variables in moose core areas ($P <$

0.02 , all cases), with the exceptions of shrub and graminoid coverage ($P = 0.14$ and 0.15 , respectively). Important similarities also were apparent. All core areas had $>70\%$ total plant coverage, $>42\%$ shrub coverage, and >3600 m³/ha in total shrub volume. Differences in areas were strongly related to elevation and community type. The MC core area, at an elevation of 2700-2800 m and dominated by Wolf's willow (*Salix wolfii*), differed from all other core areas in having less plant coverage, forb coverage, total plant volume, shrub volume, and forb volume; and less graminoid volume than one other core area (BR)(Table 3, $P < 0.05$, all cases). The 2 core areas with the highest plant and shrub volumes, EF and MB, were associated with traditional moose habitat in floodplain willow communities, and had higher values in these variables than other core areas ($P < 0.05$).

In community similarity, core areas in traditional shrub-dominated wetlands (EF and MB) or aspen-shrub communities (LR) were similar in species composition ($>45\%$, all

Table 2. Seasonal habitat selection by 3 male and 10 female moose in the Fiddler and Fishtail Creek drainages, south-central Montana, 1989-93. Numbers indicate percentages. Symbols in parentheses indicate selection for (+), selection against (-), or no selection (0). $P < 0.01$ (simultaneous confidence intervals, Marcum and Loftsgaarden 1980) for all cases of selection and for differences between sexes, except where noted.

Cover type	Available	Moose locations %				Annual		
		Winter	Spring	Summer	Autumn	M use	F use	Pattern
Aspen	17.5	43.0 (+)	40.2 (+)	56.5 (+)	36.0 (+)	60.0 (+)	40.2 (+)	M>F
Shrub-dominated wetland	8.1	23.9 (+)	20.7 (+)	8.7 (0)	17.4 ^a (0)	17.1 (0) ^a	16.5 (+)	M=F
Lodgepole	55.0	21.8 (-)	20.7 (-)	17.4 (-)	31.1 (-)	12.6 (-)	25.4 (-)	M<F
Other coniferous forest	7.5	7.7 (0)	13.2 (0)	10.9 (0)	5.0 (0)	8.0 (0)	10.0 (0)	M=F
Other non-forest	11.9	3.5 ^b (-)	5.2 (0)	6.5 (0)	10.6 (0)	2.2 (-)	7.9 (0)	M<F

^a $P = 0.06$

^b $P = 0.02$

comparisons, Table 4). The BR core area, a lower elevation range comprised of upland shrub communities dominated by chokecherry and wild plum, was less similar to other core areas (<36%, all comparisons). The high elevation willow community of the MC core area showed little similarity to any other core area (<12%, all comparisons).

Core areas differed in shrub nutritional values (Table 5), but each area displayed unique nutritional advantages compared to others. The MC core area had higher gross energy (kcal/kg) than any other core area, and the EF core area displayed higher shrub protein levels than any other area ($P < 0.05$, all comparisons). Higher Ca and P levels in shrubs were associated with the BR area ($P < 0.05$, both variables, all comparisons).

DISCUSSION

Elevation and Habitat Use

All null hypotheses regarding season- and sex-specific habitat and elevational use were rejected. Both habitat use and elevational use were different from expected, different in different seasons, and different in males and females. This suggests that, in this population, habitat and elevational use are selective, that they may be based on differing seasonal requirements in moose, and that such requirements are different in different sexes even in the same season.

Such results are consistent with studies of other cervids (Bowyer 1984, Mace *et al.* 1984, Clutton-Brock *et al.* 1987, McCullough *et al.* 1989), as well as studies of moose (Miller and Litvaitis 1992, Miquelle *et al.*

Table 3. Plant community characteristics of core foraging areas used by 5 female moose in south-central Montana, 1989-92. SE in parentheses. N=4 (EF and MB), 7 (LR and MC), or 9 (BR.) All differences $P < 0.05$.

Characteristic	Core Area											
	MC		EF		MB		LR		BR		Combined	
Plant coverage (%)	71.5 ^a	(1.7)	98.1 ^b	(1.2)	94.7	(3.0)	90.3	(2.2)	93.3	(1.8)	88.5	(5.1)
Shrub coverage (%)	53.5 ^b	(3.9)	45.3	(3.6)	53.3	(4.2)	42.5	(3.4)	49.1	(2.5)	48.7	(8.6)
Forb coverage (%)	5.6 ^a	(2.1)	24.0	(4.4)	26.0	(2.8)	32.7	(2.9)	24.8 ^b	(2.5)	22.3	(7.1)
Graminoid coverage (%)	12.8 ^c	(1.9)	17.0	(4.5)	15.2	(1.9)	14.1	(1.5)	20.5	(2.5)	16.2	(6.2)
Plant volume (m ³ /ha)	3943.2 ^a	(515.8)	13838.7 ^d	(706.3)	12751.6 ^d	(520.5)	6773.2 ^a	(433.0)	9773.2 ^a	(620.9)	8786.6	(1484.8)
Shrub volume (m ³ /ha)	3645.9 ^a	(576.7)	10981.1 ^d	(911.7)	11731.4 ^d	(556.0)	5817.3 ^a	(430.8)	8132.3 ^a	(560.3)	7512.6	(1511.2)
Forb volume (m ³ /ha)	56.6 ^a	(16.6)	643.1	(242.3)	542.2	(87.7)	497.1	(98.4)	755.3	(134.9)	502.9	(316.2)
Graminoid volume (m ³ /ha)	191.2 ^c	(67.1)	866.7	(307.7)	457.9	(58.9)	422.7	(44.0)	878.9 ^b	(183.8)	571.1	(390.7)

^a Different from all other core areas.

^b Different from LR.

^c Different from BR.

^d Different from BR, LR, and MC.

^e Different from BR and EF.

Table 4. Community similarity (%) of core foraging areas used by 5 female moose in south-central Montana, 1989-93. Number of sampled macroplots in parentheses.

Core area	Core Area			
	BR	MC	LR	MB
BR (9)	—	9.2	33.6	36.1
MC (7)	9.2	—	10.5	9.9
LR (7)	33.6	10.5	—	52.7
MB (4)	36.1	9.9	52.7	—
EF (4)	26.7	11.9	46.9	45.4

Table 5. Nutritional characteristics of shrub growth in core foraging areas used by 4 female moose in south-central Montana, 1989-93. SE in parentheses. N=8 except for LR where N=6. All differences P <0.05.

Nutritional variable	Core area									
	MC		EF		LR		BR		Combined	
% Crude protein	13.6 ^a	(.07)	16.0 ^b	(0.9)	9.7 ^b	(0.4)	12.0	(0.3)	13.0	(1.8)
Gross energy (kcal/kg)	5211.1 ^b	(34.9)	4828.4 ^b	(72.5)	4635.5	(57.6)	4629.4	(24.6)	4828.8	(137.8)
% Ca	0.64	(0.02)	0.81	(0.07)	1.10 ^b	(0.05)	1.94 ^b	(0.14)	1.12	(0.23)
% K	0.75 ^c	(0.04)	1.02 ^c	(0.09)	1.74	(0.21)	1.47	(0.01)	1.21	(0.30)
% Mg	0.15 ^d	(0.01)	0.23	(0.03)	0.21 ^c	(0.02)	0.28	(0.02)	0.22	(0.06)
% Na	0.03	(0.002)	0.03	(0.003)	0.04 ^c	(0.006)	0.02	(0.002)	0.03	(0.01)
% P	0.21 ^d	(0.02)	0.28 ^b	(0.02)	0.17 ^d	(0.01)	0.35 ^b	(0.03)	0.26	(0.06)
% moisture	64.4 ^f	(1.2)	68.4 ^c	(1.6)	65.0	(1.2)	62.7	(0.3)	65.1	(3.2)

^a Different from LR and EF.

^b Different from all other core areas.

^c Different from LR and BR.

^d Different from BR and EF.

^e Different from BR.

^f Different from EF.

1992, Cederlund and Sand 1994) which have demonstrated seasonal and sexual differences in other populations. Cederlund and Sand (1994) noted that moose in a Swedish population were spatially segregated during most of the year, as did Miquelle *et al.* (1992) for

moose in Alaska. Moose are sexually dimorphic, and the larger body size of males, with concurrently higher energy demands, could be a proximate cause of differences in habitat and elevational use in different seasons (Miquelle *et al.* 1992, Cederlund and Sand

1994).

Use of lower elevations in winter and spring coincided with selection for shrub-dominated wetlands in those seasons, characteristic of Type II moose winter ranges (floodplain, riparian communities dominated by extensive stands of willow) described by Peek (1974). The lack of selection for such habitats in summer may have been related to their lack of a well-developed canopy, creating a potential negative energy balance for moose because of higher heat loading (Renecker and Hudson 1991). Reduced temperatures at higher elevations under more well-developed forest canopy, combined with increased forage availability in forest habitats in summer, may have been more attractive to moose in this population than shrub-dominated areas, though the latter provided greater overall forage production.

Activity of moose in this population consisted primarily of extended periods of feeding and resting in riparian habitats with occasional movements through forests (primarily lodgepole) to adjacent streams. Core areas were consistently dominated by shrub communities, and 4 of 5 were associated with riparian habitats. The disproportionate use moose made of core areas was behavior consistent with an herbivore whose forage intake rate has been shown to increase linearly with resource availability (Andersen and Saether 1992). According to patch-use theory, a forager should stay in a patch until the net gain drops below the average for all patches in the habitat (Charnov 1976). The lengthy and extensive use moose made of their core areas therefore suggests an extremely high quantity and quality of forage in relation to other available habitat in the home range. Actual energy and protein levels in core area forage also suggested that forage was of high quality compared to actual moose nutrient and energy requirements (Andersen and Saether 1992). Overall, average crude protein levels in core area browse were similar to reported

crude protein levels in summer forage of moose in Alaska (Oldemeyer *et al.* 1977) and in summer diets of free-ranging cow moose in Alberta (Renecker and Hudson 1985).

Vegetative and nutritional data from the 5 core areas led to rejection of the null hypotheses that core areas did not differ from one another in vegetative or nutritional characteristics. This suggests that cow moose could meet forage requirements for themselves and their calves using a variety of browse species, though they consistently selected shrub communities as core foraging areas. In moose, variations in plant biomass may play a significant role in diet selection (Niemela and Danell 1988, Danell *et al.* 1991), and Edenius (1993) demonstrated that moose respond to variation in resource availability through adjustments in foraging behavior. Such adjustments may have enabled individual moose to use core areas with widely divergent characteristics.

Forbs and graminoids appeared to be relatively unimportant in core areas, but high shrub coverage was the one habitat component which appeared obligate for moose, with all core areas having >42% and not different from each other. Actual shrub volume was variable, indicating that availability and quality of shrub growth probably was more important than quantity. For example, the lower shrub volumes of the MC core area were characteristic of alpine shrub growth. All shrub volume in this core area was present to moose in a single, uniform layer approximately 1 m in height, and was of uniformly high energy content. Lower elevation core areas had higher shrub volumes, but much of this was only marginally available to moose because of the height, density, or growth forms of the vegetation. In addition, lower elevation forage was of lower average energy levels.

Management Implications

The more permanent seasonal ranges of

moose in this population, like those of other Shiras moose populations, favor a management system in which long-term data contribute to an accurate assessment of condition and trend in forage supplies in core use areas (Peek 1974). Moose in this population probably would benefit from preservation, enhancement, and creation of sites with >42% palatable shrub coverage and >3600 m³/ha palatable shrub volume. Even relatively small areas with such characteristics could receive disproportionately heavy use by moose.

Because of the disproportionate utilization moose in this population made of their core areas, managers of moose populations in similar habitats should consider shifting emphasis from traditional strategies of broad scale habitat management to more intensive, site specific management of areas which could provide the characteristics documented in this study. Such intensive management could prove more cost-effective than management aimed at larger land units. This may be particularly applicable for western moose populations where preferred habitats are patchily distributed. The availability of sites with characteristics similar to core areas found in this study could be enhanced in a variety of ways. On poorly drained sites or those associated with riparian areas, a combination of pothole development with timber removal or thinning could produce sites with vegetation similar to that found in these core areas. On sites with high moisture levels. However, moose in this study also made extensive use of upland sites, such as the BR core area. On upland areas with similar physical characteristics, combination treatments of burning with timber removal or thinning could effectively replicate vegetation communities with core area characteristics. Successful treatments of areas as small as 3-5 ha within moose home ranges could be expected to receive disproportionately heavy use by moose, though management of larger areas also could expect similar moose response.

ACKNOWLEDGEMENTS

This study was administered by the Montana Department of Fish, Wildlife, and Parks (MDFWP) in cooperation with the U. S. Forest Service (USFS). Major funding was provided by the USFS, the Montana Chapter of Safari Club International, MDFWP, and Northwestern College, Orange City, IA. K. Iverson, MDFWP, piloted the helicopter used in capturing moose and the fixed-wing aircraft used in most subsequent aerial locations of radio-collared moose. R. Kenyon, DVM, Conrad, MT, darted moose from the helicopter. C. E. Eustace and S. T. Stewart, MDFWP, shared previously collected information on characteristics of the study population. A. J. Johnson, Northwestern College, and S. E. Maxwell, University of Notre Dame, South Bend, IN, assisted with statistical analysis. J. M. Peek, Univ. Idaho, Moscow; L. A. Renecker, Univ. Alaska, Fairbanks; and V. Van Ballenberghe, Pacific Northwest Research Station, USFS, Anchorage, AK reviewed preliminary drafts of the manuscript.

REFERENCES

- ACKERMAN, B. B., F. A. LEBAN, M. D. SAMUEL, and E. O. GARTON. 1990. User's manual for program home range. Second ed. Tech. Rep. 15, Forestry, Wildlife, and Range Exp. Stn., Univ. Idaho, Moscow. 80pp.
- ANDERSEN, R., and B. SAETHER. 1992. Functional response during winter of an herbivore, the moose, in relation to age and size. *Ecology* 73:542-550.
- ASSOCIATION OF OFFICIAL ANALYTICAL CHEMISTS. 1965. Official methods of analysis. 10th ed. Assoc. Off. Anal. Chemists, Washington, D. C. 957pp.
- BELOVSKY, G. E., and P. A. JORDAN. 1978. The time-energy budget of a moose. *Theor. Population Biol.* 14:76-104.
- BOWYER, R. T., 1984. Sexual segregation in southern mule deer. *J. Mammal.*

- 65:410-417.
- CEDERLUND, G., and H. OKARMA. 1988. Home range and habitat use of adult female moose. *J. Wildl. Manage.* 52:336-343.
- _____, and H. SAND. 1994. Home range size in relation to age and sex in moose. *J. Mammal.* 75:1005-1012.
- CHARNOV, E. L. 1976. Optimal foraging: the marginal value theorem. *Theoretical Pop. Biol.* 9:129-136.
- CHEW, R. M., and A. E. CHEW. 1965. The primary productivity of a desert shrub (*Larrea tridentata*) community. *Ecol. Monogr.* 35:355-375.
- CLUTTON-BROCK, T. H., G. R. IASON, and F. E. GUINNESS. 1987. Sexual segregation and density-related changes in habitat use in male and female red deer (*Cervus elaphus*). *J. Zool. (London)*:211:275-289.
- DANELL, K., P. NIEMELA, T. VARVIKKO, and T. VUORISALO. 1991. Moose browsing on Scots pine along a gradient of plant productivity. *Ecology* 72:1624-1633.
- EDENIUS, L. 1993. Browsing by moose on Scots pine in relation to plant resource availability. *Ecology* 74:2261-2269.
- FRANZMANN, A. W. 1978. Moose. Pages 66-81 in J. L. Schmidt and D. L. Gilbert, eds. *Big game of North America: ecology and management*. Stackpole Books. Harrisburg, Pa. 494pp.
- GARTON, E. O., M. D. SAMUEL, and J. M. PEEK. 1985. Analysis of moose home ranges. *Alces* 21:77-89.
- HAUGE, T. M., and L. B. KEITH. 1981. Dynamics of moose populations in north-eastern Alberta. *J. Wildl. Manage.* 45:573-597.
- HAYNE, D. W. 1949. Calculation of size of home range. *J. Mammal.* 30: 1-18.
- JOHNSON, R. A. 1992. Pollination and reproductive ecology of acuna cactus, *Echinomastus erectocentrus* var. *acunensis* (*Cactaceae*). *Int. J. Plant Sci. Part I.* 153:400-408.
- KITTREDGE, J. 1945. Some quantitative relations of foliage in the chaparral. *Ecology* 26:70-73.
- LUDWIG, J. A., J. F. REYNOLDS, and P. D. WHITSON. 1975. Size biomass relationships of several Chihuahuan Desert shrubs. *Amer. Midl. Nat.* 94:451-461.
- MACE, G. M., P. H. HARVEY, and T. H. CLUTTON-BROCK. 1984. Vertebrate home range size and energetic requirements. Pages 32-53 in J. R. Swingland and P. J. Greenwood, eds. *The ecology of animal movement*. Oxford Univ. Press. Oxford, U. K. 311pp.
- MARCUM, C. L., and D. O. LOFTSGAARDEN. 1980. A non-mapping technique for studying habitat preferences. *J. Wildl. Manage.* 44:963-968.
- McCULLOUGH, D. R., D. H. HIRTH, and S. J. NEWHOUSE. 1989. Resource partitioning between sexes in white-tailed deer. *J. Wildl. Manage.* 53:277-283.
- MILLER, B. K., and J. A. LITVAITIS. 1992. Habitat segregation by moose in a boreal forest. *Acta Theriologica* 37:41-50.
- MILLS, G. S., J. B. DUNNING, JR., and J. M. BATES. 1991. The relationship between breeding bird density and vegetation volume. *Wilson Bull.* 103:468-479.
- MIQUELLE, D. G., J. M. PEEK, and V. VAN BALLEMBERGHE. 1992. Sexual segregation in Alaskan moose. *Wildl. Monogr.* 122:1-57.
- MUEGGLER, J. F., and W. L. STEWART. 1980. Grassland and shrub habitats of western Montana. U. S. For. Serv. Gen. Tech. Rep. INT-66. Ogden, Utah.
- MYTTON, W. R., and L. B. KEITH. 1981. Dynamics of moose populations near Rochester, Alberta, 1975-78. *Can. Field-Nat.* 95:39-49.
- NIEMALA, P., and K. DANELL. 1988. Comparison of moose browsing on Scots pine (*Pinus sylvestris*) and lodgepole pine (*P.*

- contorta*). J. Appl. Ecol. 25:761-775.
- NEU, C. W., C. R. BYERS, and J. M. PEEK. 1974. A technique for analysis of utilization availability data. J. Wildl. Manage. 38: 541-545.
- NIELSON, A. E., and W. M. SHAW. 1967. A helicopter-dart gun technique for capturing moose. Annu. Conf. West. Assoc. State Fish Game Comm. 47:183-199.
- OLDEMEYER, J. L., A. W. FRANZMANN, A. L. BRUNDAGE, P. D. ARNESON, and A. FLYNN. 1977. Browse quality and the Kenai moose population. J. Wildl. Manage. 41:533-542.
- PEEK, J. M. 1974. On the nature of winter habitats of Shiras moose. Naturaliste can. 101:131-141.
- _____, D. L. URICH, and R. J. MACKIE. 1976. Moose habitat selection and relationships to forest management in north-eastern Minnesota. Wildl. Monogr. 48. 65pp.
- PFISTER, R. D., B. L. KOVALCHIK, S. F. ARNO, and R. C. PRESBY. 1977. Forest habitat types of Montana. U. S. For. Serv. Gen. Tech. Rep. INT-34. Ogden, Utah.
- PIERCE, D. J., and J. M. PEEK. 1984. Moose habitat use and selection patterns in north-central Idaho. J. Wildl. Manage. 48:1335-1343.
- REGELIN, W. L., C. C. SCHWARTZ, and A. W. FRANZMANN. 1985. Seasonal energy metabolism of adult moose. J. Wildl. Manage. 49:388-393.
- RENECKER, L. J., and R. J. HUDSON. 1985. Estimation of dry matter intake of free-ranging moose. J. Wildl. Manage. 49: 785-792.
- _____, and _____. 1992. Thermoregulatory and behavioral response of moose: is large body size an adaptation or a constraint. Alces Suppl. 1:52-64.
- RISENHOOVER, K. L. 1986. Winter activity patterns of moose in interior Alaska. J. Wildl. Manage. 50:727-734.
- _____. 1989. Composition and quality of moose winter diets in interior Alaska. J. Wildl. Manage. 53:568-577.
- SAMUEL, M. D., D. J. PIERCE, and E. O. GARTON. 1985. Identifying areas of concentrated use within the home range. J. Animal Ecol. 54:711-719.
- SAS INSTITUTE INC. 1989. SAS/STAT user's guide, version 6. Fourth ed. SAS Institute Inc., Cary, N. C. 943pp.
- SCHREUDER, H. T., and M. S. WILLIAMS. 1995. Design-based estimation of forest volume within a model-based sampled selection framework. Can. J. For. Res. 25:121-127.
- SCHWARTZ, C. C., W. L. REGELIN, and A. W. FRANZMANN. 1984. Seasonal dynamics of food intake in moose. Alces 20:223-244.
- U. S. DEPARTMENT OF COMMERCE. 1992. Annual climatological summary. U. S. Dep. Comm. Natl. Oceanic and Atmos. Adm. Asheville, N. C.
- VAN BALLEMBERGHE, V., and D. G. MIQUELLE. 1990. Activity of moose during spring and summer in interior Alaska. J. Wildl. Manage. 54:391-396.
- _____, and J. M. Peek. 1971. Radiotelemetry studies of moose in north-eastern Minnesota. J. Wildl. Manage. 35:63-71.
- VANDYKE, F., B. L. PROBERT, and G. M. VAN BEEK. 1995. Moose home range fidelity and core area characteristics in south-central Montana. Alces 31:93-104.
- WHITTAKER, R. H., and G. M. WOODWELL. 1968. Dimension and production relations of trees and shrubs in the Brookhaven forest. J. For. 56:1-25.