MOVEMENTS AND HABITAT SELECTION OF SHIRAS MOOSE (*ALCES ALCES SHIRASI*) IN COLORADO

Roland C. Kufeld[1] and David C. Bowden[2]

[1]Colorado Division of Wildlife, 317 W. Prospect, Fort Collins, CO 80526, USA; [2]Department of Statistics, Colorado State University, Fort Collins, CO 80523, USA

ABSTRACT: From December 1991, through November 1995, we recorded 3,897 locations on 66 radio-collared moose (*Alces alces shirasi*) (25 males and 41 females) in northcentral Colorado, to determine seasonal movements and selection of habitat. Few significant differences (P <0.05) were found between sex or age categories in median size of seasonal minimum convex polygon (MCP) areas, or in median distances moved between seasonal median activity centers (MACs), because movement depended mainly upon characteristics of individual animals. However, subadult and adult males used larger seasonal MCP areas than females, and adults used larger seasonal MCP areas than subadults. Sixty-two percent of subadult males and 17% of subadult, females dispersed from natal areas at distances ranging from 13 to 120 km. Moose $\geq$2 years old, of both sexes occupied annual home ranges that usually included several smaller areas which the animal used seasonally. Winter MCP areas usually included lower elevations than spring, summer, and autumn MCPs suggesting most moose migrated to higher elevations in other seasons. The only significant difference (P < 0.05) between sexes in proportional use of habitat types during seasons of the year was in lodgepole pine habitat in winter. Willow (*Salix* spp.) was the most commonly selected habitat by moose in all seasons, and lodgepole pine (*Pinus contorta*) was second. Other habitat types used by moose were aspen (*Populus tremuloides*), spruce-fir (*Picea engelmannii - Abies lasiocarpa*), and grass meadow. Locations of radio-collared moose in lodgepole pine or spruce-fir usually were near willow habitat. We infer that willow habitat in riparian areas is important to maintain moose populations and should be protected from influences that could reduce its value to moose. During logging operations strips of uncut, mature timber should be maintained within 250 m of willow bottoms and clearcutting patterns should be designed to produce a mosiac of relatively large patches (> 0.7 km^2) of uncut, mature timber. We suggest that no point in a clearcut be more than 100 m from adequate hiding cover.

ALCES VOL. 32 (1996) pp.85-99

Moose in Colorado historically were rare (Warren 1942, Bailey 1944, Lechleitner 1969). In 1978 - 1979, 24 moose (*Alces alces shirasi*) were transplanted from northeastern Utah and northwestern Wyoming to North Park, in northcentral Colorado, to establish a viable population (Duvall and Schoonveld 1988). The population in North Park had grown to approximately 382 to 505 animals by 1992 (Bowden and Kufeld 1995). Subsequent transplants have been conducted to establish populations of moose in other parts of Colorado (Kufeld 1994, Olterman *et al.* 1994).

Movements and habitat relationships of moose have been studied throughout much of their range (Houston 1968, Stevens 1970, Van Ballenberghe and Peek 1971, Krefting 1974, LeResche *et al.* 1974, Peek *et al.* 1976, Doerr 1983, Pierce and Peek 1984, Cederlund and Okarma 1988, Leptich and Gilbert 1989, Cederlund and Sand 1994). Nowlin (1985) reported on pioneering movements of animals originally released in the then vacant moose habitat of North Park. Our study was initiated to determine the magnitude of seasonal movements and seasonal preference for habitat types exhibited by moose now that sufficient time has elapsed for the population in North Park to become established and to occupy available habitat. Such information will be useful to wildlife personnel concerned with habitat evaluation and improvement or with mitigation of habitat losses.

We examined the following general hypotheses: (1) distribution and movements of moose varies by sex, age, and season of year; (2) habitat selection by moose varies by sex and season of year; (3) moose exhibit a strong degree of fidelity to riparian habitats along drainages during winter census periods.

STUDY AREA

North Park, with the same boundaries as Jackson County in northcentral Colorado (41°N, 106°W), is a large, open valley almost completely surrounded by high peaks. The northern boundary is the Wyoming state line. North Park is approximately 72 km long by 64 km wide, with elevations ranging from approximately 2,400 to 4,000 m.

All radio-collared moose were captured and most remained in the eastern, southern, and central portions of North Park, Colorado. However, study animals which moved outside North Park were monitored. Terrain and habitat complexes frequented by migrants were similar to those found in North Park.

North Park contains numerous streams and rivers that support extensive stands of willow (*Salix* spp.) dominated riparian habitat. The central part of North Park consists of open, relatively flat to rolling terrain dominated by sagebrush (*Artemisia tridentata*) habitat. Willow bottoms in the lower elevations of the central part meander through the large expanses of sagebrush. At higher elevations willow bottoms are bordered by extensive forests of lodgepole pine (*Pinus contorta*), aspen (*Populus tremuloides*) or spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Aspen may grow as a relatively pure stand or occur as a sub-dominant species within a habitat of predominately lodgepole pine. There are numerous clearcuts of varying sizes within the lodgepole pine and spruce-fir habitat types. Alpine tundra occurs at the highest elevations. It is dominated by numerous species of low growing grasses and herbs. Irrigated grass meadows are common along stream bottoms at lower to intermediate elevations. Plant names are from Scott and Wasser (1980).

Mean January minimum temperatures in North Park range from -18 to -22 C and mean July maximum temperatures range from 11 to 22 C. Mean annual snowfall ranges from 1.3 to 3.8 m (Erickson and Smith 1985). Winters can be severe with long periods of low temperatures and deep snow.

METHODS

Moose were captured throughout the eastern, southern, and central portions of North Park during December 1991, January, March, October, and December 1992, and January 1994. Two methods of capture were used: (1) drugs administered in 1-cc darts fired from the ground or from a helicopter, and (2) a net fired from a helicopter (Olterman *et al.* 1994). For immobilizing adults, we used 2.7 mg carfentanil HCL (3 mg/ml) and 40 mg xylazine HCL (400 mg/ml) delivered intramuscularly; immobilization was antagonized with 500 mg naloxone HCL (50 mg/ml) delivered intravenously (IV) (150 mg) and subcutaneously (SC) (350 mg). Calves were immobilized with about 1.4 mg carfentanil HCL and 20 mg xylazine HCL IM and antagonized with 300 mg naloxone HCL (divided 100 mg IV and 200 mg SC). Penicillin, 30 cc for adults and 20 cc for calves, was given subcutaneously to help prevent infection.

Sex and age composition of captured moose was similar to composition of sex and age classification determined by previous counts in the area. Moose were considered calves during their first year, subadults on June 1 beginning their 2nd year, and adults on June 1 beginning their 3rd year. Captured moose were fitted with a numbered, cattletype, plastic ear tag in each ear, and a numbered radio collar. Numbering of the collars enabled individual identification of sighted moose without use of a radio receiver. We used expandable radio collars for calves. Each radio collar was equipped with a mortality switch that increased pulse rate of the transmitter after 5 hours of inactivity.

Radio-collared moose were located at intervals of approximately 2-weeks from December 1991 through November 1995. Most locations were from a Cessna 185 aircraft with a 2 element, "H" configuration, receiving antenna mounted on each strut. A switchbox permitted the telemetry operator to use antennas jointly or separately. Aerial locations were made from an altitude of approximately 40 m to 150 m and an airspeed of approximately 120 km/hr.

Occasionally, locations were made by radio-tracking on the ground using a 2-element, "H" configuration, receiving antenna. The signal was pursued until the animal was observed. A TR-2 receiver with a TS-1 Scanner-Programmer (Telonics, Inc., Mesa, AZ) was used for all aerial and ground tracking. Moose locations were plotted on 1:50,000 scale, U.S. Geological Survey, topographic, county maps and recorded as Universal Transverse Mercator (UTM) coordinates (Grubb and Eakle 1988) to the nearest 0.01 km. A global positioning system receiver was often used to determine coordinates of locations on the ground. Elevation for each location was determined from topographic maps. Habitat type for each moose location was also recorded. These habitat types were major vegetation communities common in North Park and surrounding areas of Colorado as described by Costello (1954). The name of each habitat type, in all cases except alpine and grass meadow, is the dominant species or genera. Where aspen grows in relatively pure stands it was considered aspen habitat. Where it occurs as a secondary species in a habitat type dominated by lodgepole pine the habitat type was considered to be lodgepole pine.

Habitat availability was determined by the Colorado Division of Wildlife satellite based global information system (GIS) (Buffington and Cade 1992). Percent composition of habitat types, in the area of North Park where 96% of moose locations occurred, was compared with percent of locations of moose (sexes combined) for each habitat type during each season by t-test.

The area encompassing all observed locations for an individual moose during a specific season of the year (winter = December - February, spring = March - May, summer = June - August, Fall = September - November) was determined using the minimum convex polygon (MCP) feature (Mohr 1947, Jennrich and Turner 1969) in version 1.2 of program McPaal (Stuwe and Blowhowiak 1986). The area encompassing observed seasonal locations for a given moose is referred to as its seasonal MCP area. We use the term "MCP area" rather than "home range" to describe the area encompassing observed locations because locations were obtained at points in time which were approximately 2 weeks apart. A median activity center (MAC) for each seasonal group of locations was computed according to procedures described by Berry *et al.* (1984). A MAC is the point with coordinates (x,y) which is closest on average to all of the locations. In other words the sum of the distances of the group of locations from the MAC point is smaller than can be obtained when compared to sum of the group's distances from any other point in x,y space. Straight line distances between seasonal MACs were computed using version 6.03 of program SAS (SAS Institute Inc. 1988).

We made comparisons between categories of sex and age for seasonal MCP area size, distances moved between seasonal MACs, seasonal elevations, and seasonal use of habitat types. We used 0.05 significance level in all statistical tests of hypotheses. Differences in use of habitat types between sexes of moose, as measured by numbers of locations per type by sex category, were compared using standard 2-sample t-tests. Differences between sexes or ages of moose in size of seasonal areas occupied, or in distances between seasonal MACs were compared using non-parametric, Mann-Whitney-Wilcoxon procedures (Gibbons 1985).

RESULTS

Sixty-six moose, (age when captured: calves = 16 males and 20 females, subadults = 1 male and 2 females, adults = 8 males and 19 females) were monitored during this study. Individuals were monitored for periods up to 4 years and 3,897 moose locations were accumulated. Logically, when calves became subadults they were included in the subadult category and, subsequently, included in the adult category when they became adults. Thus, the number and sex and age composition of moose available for comparisons is as follows: calves = 16 males and 20 females, subadults = 13 males and 18 females, adults = 20 males and 35 females.

During a test of aerial location accuracy (Kufeld and Bowden 1995) using transmitters placed at 27 locations unknown to the aerial observer, the same observer, flying in the same aircraft, at similar altitudes and airspeeds, with the same pilot as used in this study, the mean, SD, and median map distances between estimated and actual point locations were 125±90m, and 100 m, respectively. Accuracy in locating moose by aircraft probably was superior to results of this test because the animal was often seen. Based on these test results, and because of the relatively large patches of habitat involved in our study, we believe that aerial accuracy of telemetry was adequate to determine selection of habitat and sizes of areas used by individual moose.

Seasonal Movements

There were few significant differences between sex or age categories in size of seasonal MCP areas (Table 1), in distances moved between seasonal MACs (Table 2), or in elevations of seasonal MCP areas (Table 3), because behavior associated with movement was highly variable among individual moose. This variability was reflected by the range of values for seasonal MCP area size and for distances moved between seasonal MACs (Tables 1 and 2).

Size of Seasonal Minimum Convex Polygon Areas.-- Differences in median size of MCP areas of male and female calves by season were not significant (Table 1). Subadult, males had significantly larger median MCP areas than females during winter, and larger, but not significant, median MCP areas than females during other seasons. Maximum of subadult male MCP areas was larger than maximum of subadult female MCP areas during winter, summer, and autumn. Adult males consistently had larger median MCP areas during all seasons than adult females (Table 1), but these differences were not significant.

Winter MCP areas for subadults and adults were not significantly different in median size from summer MCP areas. Subadults of both sexes had larger MCP areas during winter and spring than did calves, but only the difference for male subadults vs calves during winter was significant. Adult moose of both sexes had larger MCP areas during each season than subadults, but only the difference between female adults and female subadults during autumn was significant (Table 1).

Distances Moved Between Seasonal Median Activity Centers.-- Male calves moved farther between seasonal median MACs than females and significantly farther from spring to summer and from winter to summer. Maximums of male calf movements between seasonal MACS were greater

Table 1. Comparison of seasonal minimum convex polygon areas (km^2) between male and female moose in North Park, Colorado for years 1992 - 1995.

		Males			Females			
Age[a]	Season[b]	Min.	Max.	Med.	Min.	Max.	Med.	P^c
Calves	Winter	0.1	10.3	2.2	0.1	9.2	1.0	0.698
	Spring	0.2	78.7	3.4	0.2	30.0	3.6	0.808
Subadults	Winter	1.3	180.9	8.5	0.1	21.2	4.1	0.005
	Spring	0.8	30.0	7.7	0.3	46.2	5.5	0.876
	Summer	0.1	34.9	6.1	0.1	23.4	4.5	0.285
	Autumn	0.1	351.2	8.8	0.5	23.8	6.8	0.315
	P^d Winter versus Summer			0.910			0.433	
Adults[e]	Winter	2.1	62.2	14.5	0.7	74.1	5.0	0.062
	Spring	0.2	76.8	10.9	1.0	28.5	7.3	0.241
	Summer	0.6	36.3	7.5	0.3	40.7	5.8	0.782
	Autumn	2.5	74.3	20.2	2.0	33.1	10.2	0.125
	P^d Winter versus Summer			0.068			0.790	
P^c Calves versus Subadults	Winter			0.001			0.577	
	Spring			0.164			0.323	
P^c Subadults versus Adults	Winter			0.947			0.071	
	Spring			0.209			0.362	
	Summer			0.973			0.359	
	Autumn			0.235			0.010	

[a] Sample sizes are: calves = 16 males and 20 females, subadults = 13 males and 18 females, adults = 20 males and 35 females.
[b] Seasons: Winter = Dec. - Feb.; Spring = Mar. - May; Summer = June - Aug.; Autumn = Sep. -Nov.
[c] *P* value is based on Wilcoxon ranked sum comparison of median values.
[d] *P* value is based on Wilcoxon signed rank comparison of median values.
[e] A mean seasonal minimum convex polygon area was computed for each individual adult moose for the number of years it was monitored as an adult (1 to 4 years). Then minimum, maximum and median values were determined for those means.

than those of female calves (Table 2).

Median movements of subadults between winter and spring and between spring and summer MACs (the summer when subadults became adults) were similar for males and females. Subadult males moved significantly farther than females between summer and autumn. Subadult males also moved farther than females between autumn and winter, and between winter and summer (the summer when subadults became adults) but those differences were not significant (Table 2). Eight of 13 subadult males (62%) and 3 of 18 subadult females (17%) made long distance movements, considered to represent dispersal, during their subadult year or shortly after they became adults (Table 3). Dispersal involved movement to completely different mountain ranges and different major river drainages, but to similar habitat. None of the animals returned to the area from which they dispersed during the course of the study.

Table 2. Comparison of distances moved (km) between seasonal median activity centers between male and female moose in North Park, Colorado for years 1992 - 1995.

		Males			Females			
Age[a]	Season[b]	Min.	Max.	Med.	Min.	Max.	Med.	P^c
Calves	Winter to Spring	0.1	14.5	2.1	0.1	3.6	1.3	0.175
	Spring to Summer	0.4	17.9	6.7	0.4	11.2	2.3	0.004
	Winter to Summer	0.5	15.2	8.5	0.3	8.8	2.2	0.001
Subadults	Winter to Spring	0.2	8.5	1.7	0.3	16.3	1.7	0.635
	Spring to Summer	0.6	25.6	3.8	0.3	58.2	3.8	0.239
	Summer to Autumn	0.7	75.9	3.8	0.1	23.5	1.0	0.004
	Autumn to Winter	0.4	24.7	8.8	0.3	15.0	4.6	0.224
	Winter to Summer	1.1	25.7	7.1	0.1	58.7	4.2	0.386
Adults[d]	Winter to Summer	0.6	8.4	3.6	0.1	14.4	3.3	0.810
	Spring to Summer	1.2	16.3	7.2	0.6	18.5	4.3	0.340
	Summer to Autumn	0.7	19.1	3.4	0.5	21.7	2.7	0.342
	Autumn to Winter	2.1	11.9	6.3	0.4	16.7	6.5	0.622
	Winter to Summer	1.2	18.8	5.5	1.1	18.1	5.8	0.646
P^c Calves	Winter to Spring			0.910			0.254	
versus	Spring to Summer			0.671			0.268	
Subadults	Winter to Summer			0.548			0.071	
P^c Subadults	Winter to Spring			0.286			0.174	
versus	Spring to Summer			0.901			0.311	
Adults	Summer to Autumn			0.722			0.008	
	Autumn to Winter			0.336			0.444	
	Winter to Summer			0.960			0.480	

[a] Sample sizes are: calves = 16 males and 20 females, subadults = 13 males and 18 females, adults = 20 males and 35 females.

[b] Seasons: Winter = Dec. - Feb.; Spring = Mar. - May; Summer = June - Aug.; Autumn = Sep. - Nov.

[c] *P* value is based on Wilcoxon ranked sum comparison of median values.

[d] A mean distance moved between seasonal median activity centers was computed for each individual adult moose for the number of years it was monitored as an adult (1 to 4 years). Then minimum, maximum and median values were determined for those means.

study. Median and maximum movements between seasonal MACs were similar for adult males and adult females (Table 2).

Median distances moved from winter to spring, spring to summer, and winter to summer MACs were not significantly different between calves and subadults for either sex, but subadults consistently had greater maximum movements between seasonal MACs than calves (Table 2). Median distances moved between seasonal MACs were not significantly different between subadults and adults for either sex except for the median distance moved from summer to autumn by females. Although that median distance was statistically significant the difference in km moved was small. Subadults exhibited much longer maximum movements between most seasonal MACs than did adults (Table 2). Individual adult moose demonstrated fideli-

Table 3. Distances dispersed (km) and directions of dispersal by 8 male and 3 female subadult moose radio-collared in North Park, Colorado.

Males		Females	
Distance	Direction	Distance	Direction
120	Southwest	114	North
95	North	91	Southwest
68	North	14	Southeast
27	Southeast		
21	North		
19	Northeast		
19	Southwest		
13	Southwest		

ty to winter and summer MACs during the 4 years of the study. Winter MACs for adults were a median distance of 3.6 km apart while the median distance separating summer MACs was 1.9 km.

Elevations of Seasonal Minimum Convex Polygon Areas.-- Median elevations of seasonal MCP areas of individual moose ranged from 2,465 to 3,222 m. (Table 4). The lowest location for a radio-collared moose during this study was 2,451 m, the highest was 3,487 m. Treeline for North Park is approximately 3,300 m depending on slope and aspect. Most moose, regardless of sex or age, tended to spend winters at lower elevations and move to higher elevations during spring, summer, and autumn. Some of the highest locations observed were during fall (Table 4). Seasonal migratory behavior varied with individual animals, however, as some stayed at about the same elevation year round, while others moved higher during winter and lower during summer.

Median elevations of MCPs for female calves during winter were significantly higher than for males, although the actual difference in elevation was only 86 m, and likely not biologically meaningful. The difference between male and female calves in median elevation of spring MCPs was not significant. Differences between male and female yearlings, and between male and female adults in elevations of seasonal MACs also were not significant (Table 4). Median elevations of MCPs used by calves during winter and spring were not significantly different from those used by yearlings for the same seasons. Similarly, there were no significant differences between yearlings and adults in median elevations for any of the 4 seasons (Table 4).

Seasonal Habitat Selection

The only significant difference between between males and females in proportional use of habitat types during seasons of the year was in use of lodgepole pine during winter (Table 5). No moose locations were recorded in sagebrush or alpine habitats, although sagebrush was the most common habitat in terms of availability (Table 6). Willow was the most commonly used habitat during winter, spring, and summer (Table 5). Proportion of moose locations in willow habitat was significantly greater than its GIS availability during all seasons ($P < 0.0001$). Lodgepole pine was the second most commonly used habitat during winter, spring and summer. During autumn, lodgepole pine habitat was most commonly used followed closely by willow habitat. Proportion of moose locations in lodgepole pine habitat was significantly greater than its GIS availa-

Table 4. Comparison of elevations (meters) between male and female moose in different seasons in North Park, Colorado for years 1992 - 1995.

		Males			Females			
Age[a]	Season[b]	Min.	Max.	Med.	Min.	Max.	Med.	P^c
Calves	Winter	2609	2774	2669	2557	2893	2755	0.018
	Spring	2536	2850	2682	2505	2963	2752	0.226
Subadults	Winter	2536	2854	2630	2594	2999	2699	0.260
	Spring	2559	2841	2633	2487	2822	2690	0.336
	Summer	2627	2999	2819	2499	3008	2771	0.401
	Autumn	2658	3222	2798	2646	3097	2765	0.577
Adults[d]	Winter	2525	2761	2658	2487	2790	2683	0.366
	Spring	2525	2785	2661	2486	2792	2665	0.583
	Summer	2526	3085	2777	2485	3085	2752	0.918
	Autumn	2566	2994	2798	2577	3188	2768	0.469
P^c Calves versus Subadults	Winter			0.723			0.175	
	Spring			0.314			0.267	
P^c Subadults versus Adults	Winter			0.969			0.430	
	Spring			0.839			0.310	
	Summer			0.522			0.988	
	Autumn			0.889			0.655	

[a] Sample sizes are: calves = 16 males and 20 females, subadults = 13 males and 18 females, adults = 20 males and 35 females.
[b] Season: Winter = Dec - Feb; Spring = Mar. - May; Summer = Jun - Aug; Autumn = Sep - Nov.
[c] *P* value is based on Wilcoxon ranked sum comparison of median values.
[d] A mean elevation was computed for each individual adult moose in each season for the number of years it was monitored as an adult (1 to 4 years). Then, minimum, maximum, and median values were determined for those means.

bility during all seasons ($P < 0.0001$). Aspen habitat type was the third most commonly used type during all seasons. Aspen also occurred infrequently as a secondary species within the lodgepole pine habitat type where radio-collared moose were located. Proportion of moose locations in aspen habitat was significantly less than its GIS availability during spring ($P = 0.021$). During other seasons no significant differences were found ($P > 0.092$). The spruce-fir habitat type was used during all seasons but ranked fourth in percent of moose locations. Proportion of moose locations in spruce-fir habitat was significantly less than its GIS availability during all seasons ($P < 0.0001$). Although large expanses of lodgepole pine and spruce-fir habitat occured on the study area, radio-collared moose located in these habitats were usually in close proximity to willow habitat. The study area contained many clearcuts of varying sizes, totalling approximately 50 km^2, in lodgepole pine and spruce-fir habitat, but no moose locations were recorded in them during winter or spring. Less than 1% of locations during summer and fall were in clearcuts, and proportion of moose locations in clearcuts during summer and fall was significantly less than GIS availability of clearcuts ($P < 0.0001$). Grass meadows re-

Table 5. Seasonal use of habitat by radio-collared moose in North Park, Colorado for years 1992 to 1995[a].

		% of locations by habitat type				
		Males n=25		Females n=41		
Season	Habitat type	$\bar{x}$ (%)	SD	$\bar{x}$ (%)	SD	P^b
Winter	Willow	69.9	20.9	60.1	20.7	0.076
	Lodgepole pine	23.3	16.6	33.8	19.5	0.026
	Aspen	6.0	9.5	3.7	7.3	0.306
	Spruce-fir	0.8	2.9	2.4	8.1	0.255
	Total	100.0		100.0		
Spring	Willow	64.6	25.1	60.0	22.9	0.446
	Lodgepole pine	28.4	19.0	34.3	20.7	0.195
	Aspen	5.6	8.0	3.1	7.5	0.224
	Spruce-fir	0.8	3.0	1.9	6.1	0.358
	Grass meadow	0.6	1.7	0.7	2.3	0.740
	Total	100.0		100.0		
Summer	Willow	47.7	24.2	57.5	23.9	0.548
	Lodgepole pine	39.9	20.2	31.5	18.2	0.114
	Aspen	9.5	16.1	7.0	14.6	0.544
	Spruce-fir	2.9	6.1	3.9	9.3	0.640
	Clearcut	0.0	0.0	0.1	0.7	0.324
	Total	100.0		100.0		
Autumn	Willow	38.4	24.8	42.8	22.4	0.490
	Lodgepole pine	51.9	23.5	47.0	21.1	0.415
	Aspen	4.4	5.2	6.4	11.0	0.328
	Spruce-fir	4.8	11.4	3.6	9.7	0.667
	Clearcut	0.5	1.9	0.2	1.1	0.527
	Total	100.0		100.0		

Seasons: Winter = Dec. - Feb.; Spring = Mar - May; Summer = June - Aug.; Autumn = Sep. - Nov.
[b] *P* value is based on standard, 2-sample, t-test.

ceived a proportionately small amount of use during spring when moose sought new growth of green grass. Moose were observed foraging on their front knees because the grass was so short. Proportion of moose locations in grass meadows during spring was significantly less than GIS availability of grass meadow habitat ($P < 0.0001$).

DISCUSSION

Seasonal Movements

The observed greater mobility of male moose in this study is a pattern described by other investigators (Lynch and Morgantini 1984, Cederlund and Sand 1994). However, mobile or sedentary behavior of moose in this study depended mainly upon characteristics of the individual rather than a tendency of sex or age groups to conform to consistent patterns of behavior. Movements of calves were naturally dictated by their dams. Female movement varied from sedentary to mobile. Consequently, calf movement patterns varied in a like manner, at least until

Table 6. Availability of habitat types in the area of North Park, Colorado where 96% of moose locations occurred[a].

Habitat type	Composition (%) of habitat types
Sagebrush	38.7
Lodgepole Pine	15.1
Grass meadow	12.2
Spruce-fir	9.5
Willow	8.3
Aspen	6.3
Alpine	3.6
Clearcuts[b]	2.4
Other habitats	3.9
Total	100.0

[a] Habitat availability was determined by the Colorado Division of Wildlife satellite based global information system (GIS) (Buffington and Cade 1992).

[b] Clearcuts were in lodgepole pine and spruce fir forests.

they separated from the dam at the end of their first year of life.

If an animal dispersed it did so as a subadult or shortly after becoming an adult. A similar behavior pattern was described by Mytton and Keith (1981). Both sexes dispersed, but males appeared more prone to disperse than females. Yearlings that did not disperse selected home ranges in the vicinity of where they were captured and monitored as calves. Gasaway *et al.* (1980) reported a low rate of dispersal from a low density moose population in Alaska, and suggested that a higher dispersal rate may occur in denser populations. The subadult dispersal rate we observed may be the combined result of rapid population increase (Bowden and Kufeld 1995) on sites where moose were introduced (Duvall and Schoonveld 1988), coupled with subadult moose dispersing to previously unoccupied, suitable habitat (Nowlin 1985). This suggests that a viable moose population likely will become established throughout Colorado in suitable habitat as a result of the previous strategic transplants described by Duvall and Schoonveld (1988) and Olterman *et al.* (1994).

Radio-collared moose of both sexes, 2 years old, selected well defined annual home ranges of variable size depending on characteristics of movement of individual moose. These annual home ranges often included several areas of variable size that the animal occupied seasonally (Hauge and Keith 1981), spaced at varying distances. These areas tended to be lower in elevation during winter and higher during spring, summer and autumn, indicating that most moose were seasonally migratory. The observation that most movement from autumn to winter use areas on our study area appeared related to snow depth agrees with findings of Kelsall (1969), Coady (1974), Van Ballenberghe (1977), and Sandegren *et al.* 1985). Hundertmark *et al.* (1990) reported that moose in southeastern Alaska avoided snow >80 cm deep. However, some of our radio-collared individuals appeared to migrate for reasons unrelated to snow depth, similar to migration reported for moose in southcentral Alaska (Van Ballenberghe 1977). Once areas of seasonal use were established individual moose usually exhibited fidelity to winter and summer areas, over time, consistent with that reported in other studies (Coady 1974, Van Ballenberghe 1977, Cederlund and Sand 1990). Occasionally, an individual animal would make a "trip" of short duration to a spot some distance away from one of its seasonal concentration areas but would then return.

Seasonal Habitat Selection

Because all moose locations were obtained in daylight, habitat use described herein reflected only diurnal use. Beyer and Haufler (1994) found that descriptions of habitat use patterns based on daylight made observations may differ from use patterns based on

24-hour sampling.

The importance of willow for moose has been described by numerous investigators (Phillips *et al.* 1973, Peek 1974, Ballard *et al.* 1991, Risenhoover 1989, Borkowska and Konopko 1994). In our study moose used willow extensively for both food and cover. Many individual moose were located exclusively in willow for several months or even years where extensive willow habitats occurred at lower elevations along river bottoms. These river bottoms were paralleled by vast, treeless, expanses of sagebrush habitat. No locations of moose were recorded in sagebrush during the study. It appeared that the willow habitat on our study area can supply all of the needs of moose as long as (1) willows are tall enough to provide hiding and thermal cover, and (2) the area of willow is large enough so that the habitat can adequately provide food and cover needs of the animals for a long time.

Lodgepole pine has been reported as a winter forage of moose (Harry 1957, Houston 1968, Schladweiler 1974, Ritchie 1978). Part of the relatively large amount of time radio-collared moose spent in this type may have been to forage on lodgepole pine. However, the importance of this habitat type and the spruce-fir type may be in their value as hiding and thermal cover (Schwab and Pitt 1991). Radio-collared moose locations in the lodgepole pine and spruce-fir types were usually in close proximity to willow habitat. Because the coniferous forests in North Park have very little shrub understory we believe these types were used mainly for cover and that willow provided the majority of forage. Lodgepole pine and spruce-fir forests could be important in providing cover for moose at higher elevations because: (1) willow at higher elevations was shorter than at lower elevations and offered food but little cover, and (2) the width of willow habitat along drainages decreased with elevation.

Numerous studies have reported increased use of clearcuts by moose as a result of clearcutting coniferous forests (Parker and Morton 1978, Doerr 1983, Monthey 1984, Matchett 1985, Cederlund and Okarma 1988). In those instances moose responded to a browse understory that was released by clearcutting resulting in an improved stand of forage. Matchett (1985) reported, however, that clearcuts with little or no browse regeneration were used rarely. Eason (1989) observed that moose densities were higher in ≥ 0.7 km^2 blocks of standing timber left after logging than in smaller blocks, and blocks >5.0 km^2 had higher densities of moose than did medium sized blocks. Eason (1989) attributed this to a lack of cover in logged areas and to improved access for hunters due to construction of logging roads. Because the lodgepole pine and spruce-fir forests in North Park have little browse understory to be released, recent clearcuts are nearly devoid of vegetation except for grass, new growth of lodgepole pine, and occasionally young aspen, if aspen was present before logging. This absence of food and cover likely resulted in radio-collared moose avoiding recent clearcuts.

MANAGEMENT IMPLICATIONS

Because both sexes of moose dispersed relatively long distances and in many directions as subadults, a viable moose population likely will become established throughout suitable habitat in Colorado as a result of 3 previous transplants of moose to Colorado described by Duvall and Schoonveld (1988), Kufeld (1994), and Olterman *et al.* (1994). Given the importance of willow habitat in riparian areas in providing forage as well as hiding and thermal cover for moose, we recommend that such habitat on ranges of moose be protected from all human influences which could reduce its value to moose. Such influences include over grazing by livestock, and logging and land development in close proximity to willow habitat.

Nearly all locations of radio-collared moose in lodgepole pine and spruce-fir forests were in mature timber stands and near willow habitat. This pattern of use suggests specific management constraints when logging operations are conducted in a willow-coniferous forest habitat complex where there is little or no understory browse. We suggest that logging in such habitats should: (1) maintain mature timber stands adjacent to willow bottoms, and (2) provide a mosiac of relatively large areas of uncut, mature timber. The need for maintaining old growth timber to provide cover for moose in a habitat complex similar to our study area has been supported by Tyers and Irby (1995). Hamilton *et al.* (1980) observed that 95% of all browsing activity was confined to within 80 m of cover. Mastenbrook and Cumming (1989) reported that moose used areas near corridors of residual timber within clearcuts during winter and preferred the area within 45 and 90 m of cover. Given the lack of use of clearcuts by radio-collared moose in our study we recommend that strips of uncut, mature timber be maintained within 250 m of willow bottoms, and that clearcutting be designed to result in a mosiac of relatively large patches ($\geq$0.7 km^2 and preferably > 5.0 km^2) of uncut, mature timber. We suggest that no point in a clearcut be more than 100 m from cover.

ACKNOWLEDGEMENTS

Funding was provided by Federal Aid to Wildlife Restoration Colorado Project W-153-R and the Colorado Division of Wildlife Game Cash Fund. We acknowledge efforts of the following in capturing moose: P. Bennett, J. K Bredehoft, R. B. Gill, J. I. Innes, S. M. Kerr, B. Kingan, B. J. Kraabel, W. R. Lance, M. W. Miller, S. H. Porter, D. F. Reed, D. E. Rodrigues, G. G. Schoonveld, K. F. Snyder, T. R. Spraker, S. F. Steinert, C. H. Wagner, J. W. Wenum, M. A. Wild, and C. L. Wood. Capture and handling procedures were approved by the Colorado Division of Wildlife Animal Care and Use Committee. D. J. Younkin piloted the Cessna 185 aircraft used to locate radio-collared moose. D. B. Pool and F. M. Pusateri provided GIS data. N. S. Miers, L. R. Morales, and S. W. Spinks assisted with data tabulation. S. A. Hoover, G. G. Schoonveld, and R. B. Gill were instrumental in obtaining funding. T. M. Pojar and T. E. Remington reviewed the manuscript and provided constructive comments.

REFERENCES

BAILEY, A. M. 1944. Records of moose in Colorado. J. Mammal. 25:192-193.

BALLARD, W. B., J. S. WHITMAN, and D. J. REED. 1991. Population dynamics of moose in south-central Alaska. Wildl. Monogr. 114. 49pp.

BERRY, K. J., P. W. MIELKE, and K. L. KVAMME. 1984. Efficient permutation procedures for analysis of artifact distributions. Pages 54-74 *in* H. J. Hietala, (ed.) Intrasite spatial analysis in archaeology. Cambridge Univ. Press, Cambridge, U. K.

BEYER, D. E. JR., and J. B. HAUFLER. 1994. Diurnal versus 24-hour sampling of habitat use. J. Wildl. Manage. 58:178-180.

BORKOWSKA, A. and A. KONOPKO. 1994. Moose browsing on pine and willow in the Biebrza Valley, Poland. Acta Theriol. 39:73-82.

BUFFINGTON, K., and A. L. CADE. 1992. A classified image of a 1989 thematic mapper (TM) satellite scene for North Park, Colorado. Colo. Div. of Wildlife, Wildlife Resource Information System. Unpubl. Map.

BOWDEN, D. C., and R. C. KUFELD. 1995. Generalized mark-sight population size estimation applied to Colorado moose. J. Wildl. Manage. 59:840-851.

CEDERLUND, G., and H. K. OKARMA. 1988. Home range and habitat use of adult female moose. J. Wildl. Manage.

52:336-343.

_______, and K. SAND. 1990. Philopatry and home range formation in moose. Trans. Congr. Int. Union Game Biol. 19:39. Abstract only.

_______, and _______. 1994. Home-range size in relation to age and sex in moose. J. Mammal. 75:1005-1012.

COADY, J. W. 1974. Influence of snow on behavior of moose. Naturaliste can. 101:417-436.

COSTELLO, D. F. 1954. Vegetation zones in Colorado. Pages iii-x *in* H. D. Harrington, (ed.) Manual of the plants of Colorado. Sage Books, Denver, CO.

DOERR, J. G. 1983. Home range size, movements and habitat use in two moose, *Alces alces*, populations in southeastern Alaska. Can. Field-Nat. 97:79-88.

DUVALL, A. C., and G. S. SCHOONVELD. 1988. Colorado moose: reintroduction and management. Alces 24:188-194.

EASON, G. 1989. Moose response to hunting and 1 km^2 block cutting. Alces 25:63-74.

ERICKSON, K. A., and A. W. SMITH. 1985. Atlas of Colorado. Colo. Assoc. Univ. Press; 73pp.

GASAWAY, W. C., S. D. DUBOIS, and K. L. BRINK. 1980. Dispersal of subadult moose from a low density population in Interior Alaska. Proc. N. Am. Moose Conf. Workshop 16:314-337.

GIBBONS, J. D. 1985. Nonparametric methods for quantitative analysis. Am. Sci. Press, Inc., Columbus, OH. 481pp.

GRUBB, T. G., and W. L. EAKLE. 1988. Recording wildlife locations with the Universal Transverse Mercator (UTM) grid system. USDA For. Serv. Res. Note RM-483. 3pp.

HAMILTON, G. D., P. D. DRYSDALE, and E. L. EULER. 1980. Moose winter browsing patterns on clear-cuttings in northern Ontario. Can. J. Zool. 58:1412-1416.

HARRY, G. B. 1957. Winter food habits of moose in Jackson Hole, Wyoming. J. Wildl. Manage. 21:53-57.

HAUGE, T. M., AND L. B. KEITH. 1981. Dynamics of moose populations in northeastern Alberta. J. Wildl. Manage. 573-597.

HOUSTON, D. B. 1968. The Shiras moose in Jackson Hole, Wyoming. Grand Teton Nat. Hist. Assoc. Tech. Bull. 1. 110pp.

HUNDERTMARK, K. J., W. L. EBERHARDT, and R. E. BALL. 1990. Winter habitat use by moose in southeastern Alaska: implications for forest management. Alces 26:108-114.

JENNRICH, R. I., and F. B. TURNER. 1969. Measurement of non-circular home range. J. Theoretical Biol. 22:227-237.

KELSALL, J. P. 1969. Structural adaptations of moose and deer for snow. J. Mammal. 50:302-310.

KREFTING, L. W. 1974. Moose distribution and habitat selection in north central North America. Naturaliste can. 101:81-100.

KUFELD, R. C. 1994. Status and management of moose in Colorado. Alces 30:41-44.

_______, and D. C. BOWDEN. 1995. Mule and white-tailed deer inhabiting eastern Colorado plains river bottoms. Colo. Div. Wildl. Tech. Pub. 41. 58pp.

LECHLEITNER, R. R. 1969. Wild mammals of Colorado. Pruett Publishing Co., Boulder, CO. 254pp.

LEPTICH, D. J., and J. R. GILBERT. 1989. Summer home range and habitat use by moose in northern Maine. J. Wildl. Manage. 53:880-885.

LeRESCHE, R. E., R. H. BISHOP, and J. W. COADY. 1974. Distribution and habitats of moose in Alaska. Naturaliste can. 101:143-178.

LYNCH, G. M., and L. E. MORGANTINI. 1984. Sex and age differential in seasonal home range size of moose in northcentral Alberta, 1971-1979. Alces 20:61-78.

MASTENBROOK, B., and H. CUMMING. 1989. Use of residual strips of timber by moose within cutovers in northwestern Ontario. Alces 25:146-155.

MATCHETT, M. R. 1985. Habitat selection by moose in the Yaak River drainage, northwestern Montana. Alces 21:161-189.

MOHR, C. O. 1947. Table of equivalent populations of North American small mammals. Am. Midl. Nat. 37:223-249.

MONTHEY, R. W. 1984. Effects of timber harvesting on ungulates in northern Maine. J. Wildl. Manage 48:279-285.

MYTTON, W. R., and L. B. KEITH. 1981. Dynamics of moose populations near Rochester, Alberta, 1975-1978. Can. Field-Nat. 95:39-49.

NOWLIN, R. A. 1985. Distribution of moose during occupation of vacant habitat in northcentral Colorado. Ph.D. Thesis, Colo. State Univ., Ft. Collins. 70pp.

OLTERMAN, J. H., D. W. KENVIN, and R. C. KUFELD. 1994. Moose transplant to southwestern Colorado. Alces 30:1-8.

PARKER, G. R., and L. D. MORTON. 1978. The estimation of winter forage and its use by moose on clearcuts in northcentral Newfoundland. J. Range Manage. 31:300-304.

PEEK, J. M. 1974. A review of moose food habits studies in North America. Naturaliste can. 101:195-215.

_______, D. L. URICH, and R. J. MACKIE. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. Wildl. Monogr. 48. 65pp.

PHILLIPS, R. L., W. E. BERG, and D. B. SINIFF. 1973. Moose movement patterns and range use in northwestern Minnesota. J. Wildl. Manage. 37:266-278.

PIERCE, D. J., and J. M. PEEK. 1984. Moose habitat use and selection patterns in north-central Idaho. J. Wildl. Manage. 48:1335-1343.

RISENHOOVER, K. L. 1989. Composition and quality of moose winter diets in interior Alaska. J. Wildl. Manage. 53:568-577.

RITCHIE, B. W. 1978. Ecology of moose in Fremont County, Idaho. Idaho Dep. of Fish and Game Wildl Bull. 7. 33pp.

SANDEGREN, F., R. BERGSTROM, and P. Y. SWEANOR. 1985. Seasonal moose migration related to snow in Sweden. Alces 21:321-338.

SAS INSTITUTE INC. 1988. SAS for personal computers. SAS Institute Inc. Cary, NC.

SCHLADWEILER, P. 1974. Ecology of the Shiras moose in Montana. Montana Dep. of Fish and Game Final Rep. Fed. Aid. Proj. W-98-R and W-120-R. 100 pp.

SCHWAB, F. E., and M. D. PITT. 1991. Moose selection of canopy cover types related to operative temperature, forage, and snow depth. Can. J. Zool. 69:3071-3077.

SCOTT, T. G., and C. H. WASSER. 1980. Checklist of North American plants for wildlife biologists. The Wildlife Soc. 58pp.

STEVENS, D. R. 1970. Winter ecology of moose in the Gallatin Mountains, Montana. J. Wildl. Manage. 34:37-46.

STUWE, M., and C. E. BLOWHOWIAK. 1986. Micro computer program for the analysis of animal locations. Conserv. Res. Center, Natl. Zool. Park, Smithsonian Inst., Front Royal, VA. 18pp.

TYERS, D. B., and L. R. IRBY. 1995. Shiras moose winter habitat use in the upper Yellowstone River valley prior to and after the 1988 fires. Alces 31:35-43.

VAN BALLENBERGHE, V. 1977. Migratory behavior of moose in southcentral Alaska. Int. Congr. Game Biol. 13:103-109.

______, and J. M. PEEK. 1971. Radiotelemetry studies of moose in northeastern Minnesota. J. Wildl. Manage. 35:63-71.

WARREN, E. R. 1942. The mammals of Colorado. Second revised ed. Univ. Oklahoma Press, Norman. 330pp.