RUTTING BEHAVIOR OF MOOSE IN CENTRAL ALASKA

Victor Van Ballenberghe[1] and Dale G. Miquelle[2]

[1]U.S. Forest Service, Pacific Northwest Research Station, 3301 C Street, Suite 200, Anchorage, AK 99503-3954; [2]Hornocker Wildlife Institute, P.O. Box 3246, University Station, Moscow, ID 83843

ABSTRACT: We studied rutting behavior of moose in Denali National Park , Alaska during 1980-1983 and 1986. Definitions of sex-specific behaviors are provided based on over 1,000 hours of observation. Feeding (73% of total time) dominated female behaviors. Standing, alert behavior, and moving (2-9%) were other important non-social behaviors. Time allocated to various social and non-social behaviors by males varied among lone males, males in male groups, satellite males, and dominant males that controlled female groups. Lone bulls engaged in feeding, moving, croaking, bush thrashing, and standing about 72% of the time. Dominant bulls in mixed groups engaged in threats and displays to rivals with a combined frequency of 15%. Dominant males allocated varying percentages of time to certain behaviors as the rut progressed; herding females, courtship, and fighting were rare or absent early in the rut. We determined group size for rutting aggregations of different sex-age composition during different periods of the rut (early, mid and peak rut). Median group sizes were 4, 6, and 7, respectively, during these periods, with 37 being the largest aggregation observed. We suggest that moose in this area have a highly polygynous breeding system with dominant males responsible for most of the copulations. Although dominant males defend rutting aggregations and herd females, moose do not form true harems.

ALCES VOL. 32 (1996) pp.109-130

Little is known of the social behavior or mating system of moose (*Alces alces*), in part, because they inhabit remote areas, occur at low densities, and are secretive by nature. A series of authors have provided partial descriptions of behavioral repertoires in different areas of North America (Altmann 1959, Geist 1963, de Vos *et al.* 1967, Lent 1974, Peek *et al.* 1986, Bowyer *et al.* 1994). Recently, social behavior of Alaskan moose (*A. a. gigas*) has received attention (Peek *et al.* 1986, Miquelle and Van Ballenberghe 1985, Miquelle, 1991, 1990, Miquelle *et al.* 1992, Van Ballenberghe and Miquelle 1993, Molvar and Bowyer 1994). Despite this work, there is as yet no comprehensive ethogram documenting rutting behaviors or a description of the mating system for this or any subspecies of moose.

Bull moose have been described as having well developed species-specific patterns of aggression and courtship (de Vos *et al.* 1967). Among the four extant genera of North American cervids, moose are thought to be the least gregarious (de Vos *et al.* 1967). Altmann (1959) and Geist (1963) described a mating system in which solitary cows were courted and defended by a lone bull. In Alaska, however, many authors have noted that the subspecies is considerably more gregarious (Lent 1974, Miquelle *et al.* 1992, Van Ballenberghe and Miquelle 1990, Molvar and Bowyer 1994). Group formation by Alaskan female moose would provide the opportunity for development of a polygnous, female-defense "harem-style" mating system, if bulls were able to restrict access to groups of females. There likely are costs for this opportunity of increased reproductive success. Therefore, we were particularly interested in the activity budgets of bull moose in different social contexts, compared with cows.

The objectives of this study were to describe the behavior and mating system of moose in Denali National Park and Preserve

(DNPP), Alaska. We attempted to define all behavioral acts (Martin and Bateson 1986) of both sexes to provide a catalog (Fagen and Goldman 1977) of rutting behaviors, and to determine the frequency and duration of these behaviors so that time budgets could be estimated. Comparisons of time budgets among sex and age classes provide an opportunity to assess relative costs of reproduction. Information collected on group size and composition, in concert with knowledge of the behavioral repertoire, is used as an aid to define the breeding system of Alaskan moose.

STUDY AREA AND METHODS

Approximately 200 km^2 in the eastern quarter of DNPP (150 W, 63 45' N), Alaska, served as the study area. Our observations were centered in a broad valley bordered on the south by high mountain peaks of the Alaska Range and on the north by rugged foothills. The most productive habitats for moose lie between 750 and 1200 m elevation. Black spruce (*Picea mariana*) forests exist on poorly drained sites, whereas white spruce (*P. glauca*) is dominant on drier soils. Treeline occurs at approximately 800 m, above which dense shrub communities of resin birch (*Betula glandulosa*) and willow (*Salix spp.*) occur. Miquelle *et al.* (1992) provide a detailed description of the area.

Moose in DNPP are unhunted and remarkably tolerant of humans. During the rut, bulls appeared especially insensitive to human disturbance. We believe our presence had negligible effects on the behavior of study animals.

During 1980 and 1981, a catalog of behavioral acts was constructed. We defined behavioral units as structural entities (Martin and Bateson 1986:38) and empirically identified each behavior on the basis of combinations of motor patterns (Lehner 1979), body movements, and postures of body, head, ears, and antlers. Definitions of behavioral units were based in part on descriptions in Altmann (1959), Geist (1963), de Vos *et al.* (1967), Lent (1974), and Walther (1984), but we relied mainly on our own observations because earlier catalogs and descriptions were often incomplete. Behavioral data presented here were collected between 25 August and 10 October 1982-1983. During 1982 and 1983, new behaviors were included in the catalog as they were observed and described. We measured the completeness of the behavioral catalog using Good's estimate of coverage (Fagen and Goldman 1977). For cows, 0=0.998 (N1=1, I=1683), and for bulls 0=0.999 (N1=7, I=6886).

Continuous "all-occurrences" observations were made between 25 and 100 m from a single focal animal. The sequence and duration of all behavioral acts were recorded into a cassette tape recorder. We chose to employ a continuous observation method because, while it decreased sampling efficiency, it increased the probability of obtaining a complete behavioral catalog. Activity patterns of moose alternate between well-defined periods of rest and activity. We attempted to follow individuals through entire activity periods, which averaged between 55 and 77 minutes (Risenhoover 1986, Van Ballenberghe and Miquelle 1990, Miquelle *et al.* 1992).

We used the patterning of behaviors, and the effect of sequences of behavior units on other animals to categorize behaviors in terms of consequences (Martin and Bateson 1986). Behaviors were then separated into eight descriptive categories: 1) Feeding: activities associated with biting, chewing, and moving between feeding stations; 2) Maintenance: including standing, comfort movements, defecations, urinations and drinking; 3) Threats-Displays; 4) Aggression-Fighting-Sparring; 5) Submission; 6) Wallowing-Olfactory; 7) Courtship-Copulation; and, 8) Sociality. Behaviors considered as Social were nonaggressive, nonsubmissive behaviors that were directed to or a result of

another animal's actions. For definitions of Feeding and Maintenance activities, see Risenhoover (1986), and Miquelle *et al.* (1992). With the exception of behaviors associated with Feeding, Maintenance, and Sociality, most behaviors were sex-specific.

Frequency and percentage of time spent in each behavior are based on the sum of all behaviors of all observed animals. Time budgets were based on the proportion of total observation time spent performing a behavior for each sex-age class. Kruskal-Wallis and Wilcoxon Rank Sum tests (Zar 1984) were based on the proportional amount of time study animals allocated to each behavioral act during each activity bout.

Only adults (nonyearlings) were selected for study. Classes of bulls were defined on the basis of relative antler and body size (Miquelle 1990, 1991, Miquelle *et al.* 1992). Class 1 bulls had antler spreads less than 100 cm and were relatively small in size. Class 2 bulls had antler spreads between 100 and 155 cm, and Class 3 bulls had antler spreads greater than 155 cm, and were large in body size. Differences in total number of antler tines correlated well with visual assessments of antler size (Miquelle and Van Ballenberghe 1985).

We located moose through a combination of radio-locations of 20 animals instrumented with radiocollars and visual locations of other animals in the study area. Individuals were not randomly selected for observation. Accessibility of individuals (proximity to the road) and observability (type of habitat and terrain) were important determinants. Despite these potential biases, we believe our sample is representative of the population: during two years of observation we collected data from 27 (42%) of the 64 bull moose identified on the study area. Some individuals were sampled more than once each year. Because social context, group size and composition, and social status changed daily in this population, we believe repeated samples of individuals to be only slightly autocorrelated (Molvar and Bowyer 1994).

To test for changes in behavior over time, observations were divided into three periods, reflective of important segments of the rut: Period 1(early rut): 25 August-10 September; Period 2 (mid-rut): 11-25 September, and; Period 3 (peak): 26 September to 8 October. Most mating occured during Period 3 (Miquelle 1990, 1991, Van Ballenberghe and Miquelle 1993).

Vocalizations are an important component of Courtship, Submission, and Threat-Display behaviors. Here we provide only a brief description of the most common vocalizations as they relate to these behaviors. Vocalizations always were associated with some posture or motor activity and were therefore not included in estimates of activity budgets.

Size and composition of all groups were recorded for all animals observed during the rutting period (August 25-10 October), 1980-1983 and 1986. Sampling units were defined as the first observation of an identifiable group or individual in a day. An animal was considered part of a group if located within 100 m of another moose. Groups were classified on the basis of sex-age composition into: 1) lone individuals; 2) cow groups (could include yearling bulls), 3) bull groups (only males); 4) mixed groups (at least one cow and one bull); and 5) cows with calves.

Differences in median group size and median numbers of cows in mixed groups were analyzed with Kruskal-Wallis one-way ANOVA; differences in median group sizes between early, middle, and peak portions of the rut were compared using two periods at a time with Mann-Whitney tests. Chi-square contingency tables were used to test all other group size and group composition variables.

Behavioral data were collected on cows only in mixed groups. Bulls were observed in 5 social contexts: 1) as lone animals; 2) as members of bull groups; 3) as satellite bulls

in mixed groups; 4) as the lone bull in a mixed group; and, 5) as dominant bulls in mixed groups. Outcomes of interactions with other bulls provided the basis for determining dominance status among bulls in groups (Peek *et al.* 1986, Barrette and Vandal 1986). Satellite bulls were defined as males in mixed groups that retreated or demonstrated submissive activities when approached or threatened by another bull. Social contexts 4 and 5 are similar in that the bull under observation actively defended and courted the cows he associated with, the difference being that in context 5 he was challenged by satellite bulls. We concentrated our efforts on determining activity budgets of bulls in social contexts 4 and 5.

RESULTS

Description of Behaviors

Definitions of behaviors are based on over 1,000 hours of observations during 4 rutting seasons. Frequency and duration of behaviors are based on 97.3 hours of continuous observations of focal individuals. Definitions of behaviors exhibited by bulls (or both sexes as noted) are as follows:

Displays.— Swaying gait: this behavior is performed as two, or rarely three, bulls approach and challenge each other. The gait is stiff-legged, exaggerated, and slow; head and antlers sway markedly from side to side. This display may be initiated when animals are up to 250 m apart. Bulls approach each other at an angle, rather than head-on, and may stop several times to observe and apparently appraise each other. Swaying-gait displays may terminate with retreat of one bull, or may lead to broadside displays, lateral antler displays, and fighting. This display may occur during any stage of the rut but invariably occurs as challengers confront dominant bulls during the peak of the rut.

Lateral antler display: bulls facing each other display with bodies slightly angled, and each shows the profile of his antlers. Animals are close, generally within 3 m. The head often is angled to tilt the antlers. Ears are back and down and eyes are focused on the opponent. This display occurs as a preliminary to fighting and during pauses in extended fights and is often followed by vigorous bush thrashing. Broadside display: this is performed as a bull orients his body perpendicularly to another moose of either sex and remains motionless with head up and ears back. Hair on the dorsal midline may be erect.

Threats.— Bush thrashing: a bull lowers its antlers to a tree or shrub and rakes the plant with side-to-side movements of the head. This act may occur in isolation as the bull moves and croaks in search of other moose, may be directed at females or satellite males, or may be interspersed with lateral antler displays and antler clashing during extended fights. Antler threat: a bull draws its chin in and tips its antlers in the direction of another moose of either sex. This display is usually performed during an approach. Head-low threat: an initiator faces a recipient and lowers its head below the midline with ears back. The hair on the dorsal midline is often erect. If the recipient does not retreat, a charge often follows this threat. Kick: a moose lifts its front leg and lashes out at a recipient. This is an uncommon act for antlered bulls. Rush: a bull runs toward another moose of either sex. Head is initially high with ears back but may be lowered with antlers tipped toward the recipient upon close approach. Rushes may be low-intensity consisting of only a few steps, or may involve a chase of up to 100 m. A rush usually ends when the recipient retreats, but antler contact with the recipient's body may occur. Rush threats are most commonly initiated by dominant bulls and directed toward satellite bulls during the rut's peak.

Sparring/Fighting.— Present antlers: an initiator approaches the front of a recipient and lowers its antlers as if to solicit sparring or in

preparation for more serious antler contact. Antler push: Two bulls engage their antlers and try to push each other back during either sparring or fighting. Antler clash: violent engaging of antlers by bulls during a fight. Clashes are preceded by several quick steps if the bulls are not close and are followed by pushing. Clashes do not occur with sparring. Pawing: a bull strokes the ground with a foreleg during an extended fight or during pit digging. Pawing usually accompanies lateral antler displays. Goring: a bull engages in high intensity efforts to thrust his antlers into his opponent's body. Goring occurs if the recipient's neck is twisted sufficiently to break antler contact and the initiator drives forward and makes antler or body contact. Goring also occurs when the recipient whirls and attempts to retreat while the initiator drives his antlers into the recipient's rump. Goring does not occur during sparring. Pursuit: this consists of chasing and following of a fight's loser by its winner. Losers may retreat 200-300 meters and be escorted at a distance by the winner. If a dominant bull is displaced from a breeding aggregation, the winner may end pursuit by digging a pit or may immediately court and test cows. Jousting: Two bulls engage in antler contact without pushing.

Courtship/Testing/Copulation.— Herding: bulls chase cows or attempt to block their movement to prevent their departure from a mating aggregation. Bulls may pursue a cow up to 300 m and perform rush threats to discourage their departure. Tongue flicking: rapid licking movements of the tongue performed by bulls during courtship. This act may be accompanied by croaking or by a low stretch approach. Low stretch: an initiator approaches a cow, usually from behind, with slow, deliberate movements. Head is high with antlers laid back and ears are back. Often, a low stretch is accompanied with tongue flicking and soft croaking. If the recipient stands, the bull often terminates a low stretch approach with a naso-genital test. Naso-genital test: an initiator smells the recipient's anal-genital area. Flehmen often follows. Flehmen: a bull extends his head with muzzle up, curls his upper lip, and either remains motionless for 10-60 seconds or gently sways his muzzle back and forth. This behavioral act is associated with smelling a cow's urine on the ground or smelling a cow's genital area. Head bob: an initiator tries to cause a lying cow to stand by moving his head up and down. If the recipient stands, the initiator attempts a low stretch approach and naso-genital test. Muzzle contact: a bull establishes muzzle contact with another moose in other than the nasal or genital regions. Naso-naso contact: an initiator and a recipient smell each other's muzzle region. Cows often circle following an attempted mounting and extend their muzzle toward the bull in a head-low posture. Female rub: a cow rubs her head on a bull's shoulder-flank area. Female rubbing may precede mounting or may follow mounting attempts prior to copulation. Chinning: a bull rests his jaw on the rump or back of a cow, often with a light bouncing motion. If a cow stands following naso-genital testing, a bull executes chinning prior to mounting. Mounting: a bull balances his ventral chest area on a cow's rump, clasping her with his forelegs. The recipient may stand or move off causing the bull to follow by walking solely with his rear legs. Copulation: successful penile intromission. Copulation may occur on the first mount or may require several mountings. One pelvic thrust occurs and the bull's rear legs rarely leave the ground.

Vocalizations.— Croak: this is grunting performed repeatedly as bulls travel alone, court cows, or respond to a rival male. Croaks may be forceful and very loud, or low and soft, with the latter typical of courting and accompanied by a low stretch approach. Various types of croaking may be addressed to bulls or cows. Submissive whine: a high-pitched,

nasal moan performed by the submissive recipient of a threat or display. Bulls performing whines invariably terminate their own threats or displays and retreat if pressed.
Wallowing Acts.— Pit digging: an animal paws the ground with its foreleg using several strokes, then switches legs and attempts to dig a shallow, elongated depression. Digging is often interrupted by several attempts to urinate in the pit with a characteristic squatting posture achieved by markedly lowering the rump. Unsuccessful urination attempts are followed by renewed digging. Splashing: an animal slams its forefeet into a rutting pit following urination. Bulls lower their heads and rock their antlers from side-to-side as they splash with alternating forefeet. Urine-mud mixtures are splashed onto the antlers, head, neck and bell by this act. Wallowing (both sexes): a moose lies in a rutting pit and may shift its body position with agitated movements. Splashing and wallowing do not invariably follow pit digging and urination; during the peak of the rut bulls commonly fail to perform these acts in sequence.
Other Acts.— Clean velvet: a bull's antlers are vigorously rubbed against trees or shrubs to strip them of skin. When antlers are mature and hard, bulls actively remove their "velvet" covering with a rubbing process that may take several hours. Eat velvet: a moose ingests small strips of antler velvet adhering to shrubs or the ends of long strips still attached to its own antlers. Approach: a moose moves directly toward another animal with no obvious threat or display. Retreat: an animal moves away from another moose following a behavioral act. The movement can be a walk, run, or trot and can be for a few meters or a considerable distance. Eye aversion: the recipient of a threat or display looks away from the initiator. Rub antlers/body/tree: an animal selects a small tree and repeatedly rubs a portion of its body. Frequently, rubbing occurs in a social setting and animals attempt to displace others to appropriate the tree for their own use. Moose rub the side of their face or their neck with long, slow, up-and-down strokes. Vacuo-ejaculate: a bull with an erect penis arches its back and ejaculates.

Cow Behaviors

Threats.— Head-high threat: a cow's head is held high and back, ears are flat against the neck and down, and white hair at the base of ears is visible. This is the most common threat posture of cows toward nearby moose. If the recipient does not retreat, head-high threats are often followed by kicking or flailing. Cows most often direct this threat at other cows but may also threaten yearling bulls that attempt courtship. Flail: an animal rears on its hind legs and strikes at a recipient with very quick foreleg movements.
Vocalizations.— Moan: a high-pitched wailing that is quite variable but usually with a descending pitch at the end. Moans are similar to male whines but are more extended. Moans may be very long, loud, and quavering, or may be short and soft. Moans are most often produced in response to approach by a bull.
Courtship.— Body rub: a cow rubs its face, neck, shoulder, or flank against a bull engaged in courtship. Body rubbing may occur early in the courtship/testing/ copulation sequence or may occur following repeated mountings as the cow moves away from the bull and circles. Naso-body contact with bull: A cow's nose contacts a bull's body other than in the region of the muzzle.
Wallowing Acts.— Paw in pit: an animal strokes the surface of a rutting pit with a forefoot several times, then switches legs and repeats. No effort is made to splash or to tilt the head. Smelling the pit usually follows this act. Splashing: this is similar to the behavior by bulls including slamming a forefoot into a pit, lowering the outstretched head, and tilting the head from side to side.

An animal splashes several times with one forefoot, then uses the other forefoot and repeats the act. Wallowing: this is similar to the behavior by bulls including agitated movements while lying in a pit. Cows may extend their heads and roll onto their sides in a pit and may rise, splash, and assume a new position while lying back down. This sequence may be repeated several times in the absence of other cows or may be brief as cows threaten and displace each other. If a cow has a 6-month old calf, it may join the cow in the pit, usually at the rear of the female.

We have included alert behavior and moving (not associated with feeding) in this category because much of the time spent in these activities during the rut is the result of interactions with other moose.

Activity Budgets

Cows.— Our pooled data on cows represents a wide variety of different ecological and social circumstances experienced by cows during the entire rutting period. We generally observed cows in the presence of other moose and without calves because cows with calves were rare and generally avoided social contact. Cows without calves frequently associated with bulls, even during the earliest stages of the rut.

Feeding, moving, standing, or alert behavior composed about three quarters of all observed behavioral acts of cows (Table 1). All other activities, including social behavior, were observed rarely, even during the peak of the rut. Feeding was the most frequently observed behavior (n=612; 36%); we detected no change in feeding frequency as the rut progressed. Observing other moose, retreating, moaning, head-high threats, and various combinations of these were the most frequently observed acts associated with social behavior.

Feeding dominated all other activities when expressed on a time basis (73%, Table 1). Standing, alert behavior, and moving (2-9%), were other important nonsocial behaviors. Moaning and various combinations of moaning with feeding, threatening, retreating, and courtship (≈2%), were the predominant social behaviors on the basis of time. Mean duration of occurrence for feeding was much longer (2.19 min) than for most other behaviors except for tree rubbing (1.98 min). Other behaviors of relatively long mean duration included moaning, standing/masticating, body rubbing, and pawing in rutting pits. Behaviors of relatively short mean duration (≤1 min) included all of the threats and displays and some of the courtship behaviors including copulation.

Lone Bulls.— Bull moose were infrequently observed alone during the rutting period. Consequently, our sample of behavioral observations is much smaller for lone bulls than for bulls associated with other bulls or for bulls in mixed groups (Table 2). When alone, bulls frequently searched for other moose as demonstrated by their most common behaviors including moving, feeding and moving, moving and croaking, alert behavior, and bush thrashing. These behaviors, combined with standing, dominated all other activities on both frequency (80%) and time (72%) scales. We have included some instances of social behavior in Table 2 for lone bulls to include observation periods when bulls were initially alone but subsequently encountered other moose.

Bulls in bull groups.— Although mature bulls commonly associated exclusively with other bulls early in the rut they rarely did so during the rut's peak. Nonetheless, younger bulls, especially yearlings, frequently associated with each other as they were excluded from rutting by the dominant bulls. Our pooled data on bulls in bull groups are quite evenly divided between early (51%) and peak (48%) periods in the rut's progression with relatively few observations during mid-rut.

The most frequent behavioral acts of

Table 1. Frequency, total elapsed time, and mean duration of rutting behaviors of female moose, Denali National Park and Preserve, Alaska,1982-83, based on 1820 minutes of observation.

Category Behavior	Frequency	% Time	Duration (min)		
			n	$\bar{x}$	SE
FEEDING					
Feeding	612	72.5	592	2.19	0.12
MAINTENANCE					
Alert	309	5.4	309	0.32	0.03
Move	103	1.9	103	0.34	0.04
Stand	238	9.4	235	0.72	0.07
Comfort movement	2	<0.1	2	0.07	0.02
Defecate	2	<0.1	2	0.13	0.03
Urinate	11	0.2	11	0.25	0.07
Drink	4	<0.1	4	0.33	0.11
SOCIAL					
Observe moose	110	2.5	110	0.41	0.07
Naso-naso greeting	9	0.1	8	0.28	0.09
Approach moose	15	0.3	11	0.39	0.13
Tree rub	14	1.4	13	1.98	0.68
THREATS/DISPLAYS					
Head-high threat	39	0.3	34	0.14	0.03
Head-low threat	1	<0.1	1	0.68	—
AGGRESSION					
Rush	16	0.1	14	0.16	0.06
Kick	10	<0.1	6	0.21	0.07
Flail	2	<0.1	2	0.13	0.08
SUBMISSIVE					
Retreat	81	1.7	50	0.44	0.13
Moan-observe moose	18	0.4	18	0.45	0.08
Moan-Stand	35	2.4	35	1.27	0.47
COURTSHIP/COPULATION					
Naso-body contact	4	<0.1	4	0.05	0.01
Body rub	5	0.3	5	1.01	0.30
Allow naso-genital test	14	0.1	14	0.17	0.05
Allow chinning	10	0.1	9	0.30	0.10
Copulate/Allow mounting	3	<0.1	3	0.08	—
WALLOW/OLFACTORY					
Smell ground	2	<0.1	2	0.55	0.45
Splash or paw in pit	10	0.3	9	0.48	0.29
Wallow	10	0.3	10	0.58	0.18
TOTAL	1683	100.0			

Table 2. Frequency and time statistics for various rutting behaviors for lone bull moose, and bulls in bull groups, Denali National Park, Alaska, 1982-1983.

	Lone bulls					Bulls in bull-only groups				
		Obs. time (min)		Duration (min)			Obs. time (min)		Duration (min)	
Behavior	*n*	Total	%	$\bar{x}$	SE	*n*	Total	%	$\bar{x}$	SE
Feed and move	19	17.6	9.6	1.36	0.71	116	242	17.6	2.22	0.57
Feed/croak	—	—	—	—	—	10	8.8	0.6	0.88	0.19
Move	64	19.3	10.5	0.42	0.05	79	28.5	2.1	0.38	0.05
Move/croak	45	20.6	11.2	0.48	0.08	36	18.3	1.3	0.51	0.09
Alert	61	42.4	23.2	0.80	0.16	39	40.3	2.9	1.03	0.58
Alert/croak	4	6.5	3.5	1.61	0.83	1	0.3	0.02	0.25	—
Stand	36	24.8	13.6	0.69	0.21	210	223.1	16.2	1.08	0.18
Stand/croak	—	—	—	—	—	1	0.1	0.01	0.17	—
Croak	—	—	—	—	—	1	0.6	0.04	0.58	—
Comfort movement	6	9.0	4.9	1.51	1.05	2	0.4	0.03	0.21	0.01
Drink/eat snow	4	1.8	1.0	0.45	0.18	5	6.2	0.4	1.24	0.47
Defecate	1	0.2	0.1	0.2	—	3	1.5	0.1	0.51	0.32
Urinate	—	—	—	—	—	6	3.8	0.3	0.63	0.14
Attempt urination	—	—	—	—	—	7	0.7	0.05	0.09	0.02
Observe moose	5	13.2	7.2	2.65	1.27	19	7.6	0.5	0.4	0.08
Swaying gait	12	5.6	3.1	0.47	0.10	58	38.2	2.8	0.70	0.20
Lateral antler display	7	6.9	3.7	1.0	0.29	215	96.8	7.0	0.46	0.03
Bush thrash	25	7.4	4.0	0.30	0.05	163	79.1	5.7	0.51	0.08
Antler threat	—	—	—	—	—	2	1.5	0.1	0.74	0.24
Head low threat	—	—	—	—	—	1	0.3	0.02	0.25	—
Antler push	—	—	—	—	—	66	19.8	1.4	0.31	0.04
Antler clash	—	—	—	—	—	22	9.7	0.7	0.46	0.44
Break antler contact	—	—	—	—	—	103	2.4	1.8	0.25	0.03
Gore rival	—	—	—	—	—	—	—	—	—	—
Attempt goring	—	—	—	—	—	—	—	—	—	—

Table 2. continued...

Behavior	Lone bulls					Bulls in bull-only groups				
		Obs. time (min)		Duration (min)			Obs. time (min)		Duration (min)	
	n	Total	%	$\bar{x}$	SE	*n*	Total	%	$\bar{x}$	SE
Receive goring	—	—	—	—	—	—	—	—	—	—
Pursuit of male	—	—	—	—	—	—	—	—	—	—
Push/joust	—	—	—	—	—	8	1.4	0.1	0.18	0.03
Joust	—	—	—	—	—	325	315	22.9	0.98	0.66
Clean velvet	—	—	—	—	—	—	—	—	—	—
Eat velvet	—	—	—	—	—	1	1.4	0.1	1.4	—
Paw/dig pit	7	2.5	1.3	0.35	0.19	201	19.4	1.4	0.10	0.01
Smell pit	1	0.1	0.03	0.05	—	—	—	—	—	—
Splash in pit	—	—	—	—	—	3	0.7	0.1	0.24	0.03
Wallow	—	—	—	—	—	4	27.7	2.0	6.91	2.74
Herd cow	—	—	—	—	—	—	—	—	—	—
Tongue flick/stand	—	—	—	—	—	—	—	—	—	—
Stand/croak/flick tongue	—	—	—	—	—	—	—	—	—	—
Approach	—	—	—	—	—	15	7.3	0.5	0.56	0.09
Approach/croak	—	—	—	—	—	—	—	—	—	—
Approach/ears back	—	—	—	—	—	—	—	—	—	—
Smell cow bed	—	—	—	—	—	1	0.6	0.05	0.63	—
Head bob	—	—	—	—	—	—	—	—	—	—
Muzzle contact	—	—	—	—	—	—	—	—	—	—
Naso-naso greeting	—	—	—	—	—	—	—	—	—	—
Rub antlers/body/tree	—	—	—	—	—	—	—	—	—	—
Low stretch	—	—	—	—	—	4	2.6	0.2	0.65	0.27
Smell urine	—	—	—	—	—	4	0.9	0.1	0.45	0.05
Smell ground	1	0.2	0.09	0.17	—	—	—	—	—	—
Flehmen	—	—	—	—	—	4	0.8	0.1	0.41	0.01
Attempt N-G test	—	—	—	—	—	—	—	—	—	—

Table 2. continued...

	Lone bulls					Bulls in bull-only groups				
		Obs. time (min)		Duration (min)			Obs. time (min)		Duration (min)	
Behavior	*n*	Total	%	$\bar{x}$	SE	*n*	Total	%	$\bar{x}$	SE
Naso-genital test (N-G)	—	—	—	—	—	—	—	—	—	—
N-G test and chinning	—	—	—	—	—	—	—	—	—	—
Attempt chinning	—	—	—	—	—	—	—	—	—	—
Chinning	—	—	—	—	—	—	—	—	—	—
Stand/female rub	—	—	—	—	—	—	—	—	—	—
Mount	—	—	—	—	—	—	—	—	—	—
Copulate	—	—	—	—	—	—	—	—	—	—
Vacuo-ejaculate	—	—	—	—	—	1	0.1	0.00	0.05	—
Observe moose/ submissive whine	2	0.5	0.3	0.25	0.15	12	10.5	0.8	0.87	0.27
Submissive whine	1	0.3	0.2	0.30	—	13	4.4	0.3	0.34	0.11
Eye aversion	3	1.8	1.0	0.61	0.31	7	2	0.1	0.29	0.11
Eye aversion/whine	1	0.4	0.2	0.42	—	1	1.3	0.1	1.33	—
Stand/whine	—	—	—	—	—	11	34.5	2.5	3.14	0.73
Whine/retreat	5	1.55	0.8	0.31	0.09	14	10.7	0.8	0.76	0.27
Retreat	1	0.1	0.06	0.12	—	18	5.8	0.3	0.34	0.08
Approach/whine	—	—	—	—	—	1	0.1	0.01	0.08	—
Whine/joust	—	—	—	—	—	2	1.9	0.1	0.96	0.29
Whine/present antlers	—	—	—	—	—	2	1	0.1	1.17	—
Totals	313	183.1				1993	1377.0			

bulls in bull groups were jousting (16%), lateral antler displays (11%), standing (11%) pawing and digging rutting pits (10%), and bush thrashing (8%). No single behavior was clearly dominant. Other frequently performed behaviors included presenting antlers, feeding and moving, and behaviors associated with antler contact. Feeding and moving, standing, and jousting together composed over half (57%) of the time that bulls in bull groups allocated to different activities.

Satellite bulls.— We observed up to 8 satellite bulls at the periphery of a rutting group interacting with each other or with cows from the group when the dominant bull was otherwise occupied. Satellites persistently tried to enter the group and court cows; on occasion they were successful in their attempts to mate (Van Ballenberghe and Miquelle 1993). Because we generally focused on dominant bulls our data are few on behavior of satellites.

Bulls at the periphery of rutting aggregations most frequently stood or challenged other bulls and often retreated when challenged by the dominant bull (Table 3). Courtship behavior including naso-genital testing, chinning, and mounting occurred with relatively high frequency. Feeding and moving was the single most important behavioral act on the basis of time (22%).

Dominant bulls.— Dominant bulls are large, mature males in charge of rutting aggregations. They engage in a wide variety of behaviors including courtship and mating of cows interspersed with threats and displays directed at satellite bulls. On occasion they engage in violent fights to defend their status against rivals that themselves wish to take possession of the group. We recorded over 4,200 observations of 57 different behaviors for dominant bulls. Time expended by bulls on these behaviors totaled nearly 66 hours. About one-half of our total observations occurred during the peak of the rut.

Dominant bulls displayed a high frequency of standing (22%), moving and croaking (14%), and moving (9%) as they remained in control of their rutting aggregations (Table 3). Standing occupied 41% of their active time. Displays and threats to rivals including swaying gaits, rushes, bush thrashing, and the various fighting behaviors had a combined frequency of 15% with rushes and bush thrashing dominating these activities. Not all bush thrashing was likely directed at bulls. Dominant bulls seemed at times to direct this behavior toward cows, or at least perform it in the absence of nearby bulls.

Courtship and testing behaviors, including copulation and the events that immediately precede it, had a combined frequency of 14 percent. Low stretch approaches, naso-genital tests, tongue flicking, and standing behavior dominated courtship and testing. Dominant bulls allocated approximately equal amounts of active time to aggressive behavior and courtship (6% and 8%, respectively).

Time-Related Changes in Behavior

Dominant bulls in mixed groups allocated varying percentages of time to certain behaviors as the rut progressed. During the early rut (Period 1) certain courtship and fighting behaviors were absent including low-stretch approaches, mounting, copulation, antler clashes, and various combinations of goring. Similarly, dominant bulls were not observed herding cows during this period. Absence of these behaviors during Period 1 is related to the timing of female estrus which peaks about 1 October (Van Ballenberghe and Miquelle 1993) and is accompanied by increased intensity of courtship and rivalry between bulls. During mid-rut (Period 2), mounting, copulation and goring were again absent along with cleaning of velvet, an activity that is largely complete for mature bulls by 10 September (Van Ballenberghe 1982). Dominant bulls did not display velvet cleaning, vacuo-ejaculation, or herding of

Table 3. Frequency and time statistics for various rutting behaviors for satellite bulls in mixed groups and dominant bulls, Denali National Park, Alaska, 1982-1983.

	Satellite Bulls/Mixed Groups					Dominant Bulls/Mixed Groups				
		Obs. time (min)		Duration (min)			Obs. time (min)		Duration (min)	
Behavior	*n*	Total	%	$\bar{x}$	SE	*n*	Total	%	$\bar{x}$	SE
Feed and move	15	51.7	22.2	2.59	0.96	136	223.5	5.7	1.67	0.23
Feed/croak	—	—	—	—	—	6	56.3	1.4	9.39	5.66
Move	20	28.2	12.1	0.74	0.14	376	188.3	4.8	0.51	0.04
Move/croak	1	1.9	0.8	0.63	0.16	591	430.2	10.9	0.74	0.05
Alert	10	8.0	3.4	0.44	0.21	249	158.7	4.0	0.67	0.05
Alert/croak	—	—	—	—	—	11	10.4	0.3	0.94	0.20
Stand	34	18.9	8.1	0.56	0.11	941	1614.0	40.9	1.73	0.36
Stand/croak	—	—	—	—	—	148	248.3	6.3	1.69	0.25
Croak	—	—	—	—	—	10	1.6	0.04	0.26	0.16
Comfort movement	—	—	—	—	—	26	12.4	0.3	0.48	0.13
Drink/eat snow	—	—	—	—	—	30	21.0	0.5	0.73	0.10
Defecate	—	—	—	—	—	2	0.3	0.01	0.17	0.08
Urinate	3	0.5	0.2	0.26	0.16	18	3.0	0.1	0.34	0.04
Attempt urination	4	0.6	0.3	0.15	0.05	45	3.7	0.1	0.21	0.02
Observe moose	22	6.2	2.7	0.28	0.05	17	18.8	0.48	1.11	0.35
Swaying gait	26	11.9	5.1	0.54	0.11	69	48.9	1.2	0.72	0.12
Lateral antler display	28	12	5.2	0.47	0.14	8	9.9	0.3	1.24	0.42
Bush thrash	19	5.3	2.3	0.31	0.06	284	126.2	3.2	0.46	0.03
Antler threat	—	—	—	—	—	12	3.8	0.1	0.35	0.09
Head low threat	—	—	—	—	—	—	—	—	—	—
Rush	—	—	—	—	—	201	31.3	0.8	0.16	0.03
Kick	1	0.2	0.1	0.22	—	—	—	—	—	—
Broadside display	—	—	—	—	—	66	156.9	4.0	2.45	0.39
Present antlers	16	8.9	3.8	0.64	0.34	3	0.7	0.2	0.22	0.18
Antler push	3	0.9	0.4	0.31	0.07	16	2.2	0.1	0.14	0.02
Antler clash	2	0.03	0.01	0.02	—	20	1.0	0.03	0.05	0.01
Break antler contact	7	0.9	0.04	0.13	0.04	19	2.4	0.1	0.13	0.03

Table 3 Continued...

Behavior	Satellite Bulls/Mixed Groups					Dominant Bulls/Mixed Groups				
		Obs. time (min)		Duration (min)			Obs. time (min)		Duration (min)	
	n	Total	%	$\bar{x}$	SE	*n*	Total	%	$\bar{x}$	SE
Gore rival	—	—	—	—	—	3	0.2	0.01	0.07	0.02
Attempt goring	—	—	—	—	—	1	0.1	0.001	0.05	—
Receive goring	—	—	—	—	—	1	0.2	0.01	0.22	—
Pursuit of male	—	—	—	—	—	8	10.2	0.3	1.27	1.03
Push/joust	—	—	—	—	—	—	—	—	—	—
Joust	16	30.0	12.9	2.51	2.29	16	3.5	0.1	0.29	0.07
Clean velvet	—	—	—	—	—	11	7.4	0.2	0.67	0.18
Eat velvet	—	—	—	—	—	—	—	—	—	—
Paw/dig pit	22	4.0	1.7	0.19	0.05	79	48.9	1.2	0.94	0.18
Smell pit	—	—	—	—	—	—	—	—	—	—
Splash in pit	1	0.2	0.1	0.18	—	13	1.5	0.04	0.21	0.07
Wallow	2	4.8	2.1	2.42	1.87	7	9.6	0.2	1.59	0.71
Herd cow	—	—	—	—	—	17	15.2	0.4	0.89	0.40
Tongue flick/stand	—	—	—	—	—	104	121.3	3.0	1.20	0.18
Stand/croak/flick tongue	—	—	—	—	—	31	56.6	1.4	1.83	0.28
Approach	24	9.2	4.0	0.44	0.09	75	48.2	1.2	0.64	0.13
Approach/croak	1	0.5	0.2	0.50	—	20	22.1	0.6	1.11	0.38
Approach/ears back	—	—	—	—	—	1	0.2	0.004	0.17	—
Smell cow bed	—	—	—	—	—	2	1.4	0.04	0.69	0.23
Head bob	—	—	—	—	—	1	0.4	0.01	0.42	—
Muzzle contact	—	—	—	—	—	6	2.7	0.1	0.53	0.19
Naso-naso greeting	—	—	—	—	—	8	1.2	0.03	0.16	0.03
Rub antlers/body/tree	4	0.1	—	—	—	—	—	—	—	—
Low stretch	7	6.1	2.6	0.87	0.30	191	88.6	2.3	0.49	0.03
Smell urine	2	0.6	0.3	0.30	0.10	48	24.8	0.6	0.54	0.11
Smell ground	—	—	—	—	—	9	27.8	0.7	3.09	2.57
Flehmen	4	0.9	0.4	0.22	0.13	54	26.4	0.7	0.52	0.04

Table 3 Continued...

Behavior	Satellite Bulls/Mixed Groups					Dominant Bulls/Mixed Groups				
		Obs. time (min)		Duration (min)			Obs. time (min)		Duration (min)	
	n	Total	%	$\bar{x}$	SE	*n*	Total	%	$\bar{x}$	SE
Attempt N-G test	—	—	—	—	—	22	5.2	0.1	0.25	0.06
Naso-genital test (N-G)	15	2.5	1.1	0.23	0.08	106	27.0	0.7	0.26	0.04
N-G test and chinning	—	—	—	—	—	5	3.4	0.1	0.85	0.60
Attempt chinning	—	—	—	—	—	2	0.4	0.01	0.19	0.06
Chinning	15	6.4	2.8	0.46	0.11	45	11.6	0.3	0.29	0.04
Stand/female rub	2	0.4	0.2	0.19	0.13	3	1.4	0.04	0.46	0.10
Mount	10	1.6	0.7	0.18	0.11	14	1.3	0.03	0.09	0.02
Copulate	—	—	—	—	—	6	0.5	0.01	0.09	0.02
Vacuo-ejaculate	—	—	—	—	—	2	1.5	0.04	0.75	0.58
Observe moose/ submissive whine	—	—	—	—	—	—	—	—	—	—
Submissive whine	—	—	—	—	—	—	—	—	—	—
Eye aversion	3	2.5	1.1	0.84	0.67	—	—	—	—	—
Eye aversion/whine	—	—	—	—	—	—	—	—	—	—
Stand/whine	1	0.1	0.04	0.08	—	—	—	—	—	—
Whine/retreat	1	0.2	0.1	0.17	—	—	—	—	—	—
Retreat	21	6.5	2.8	0.43	0.23	—	—	—	—	—
Approach/whine	—	—	—	—	—	—	—	—	—	—
Whine/joust	—	—	—	—	—	—	—	—	—	—
Whine/present antlers	—	—	—	—	—	—	—	—	—	—
Totals	362	232.8				4215	3944.0			

cows during the peak of the rut (Period 3).

We detected four basic patterns in the mean percentage of time dominant bulls devoted to certain behaviors during the three periods of the rut (Table 4). First, time devoted to courtship and fighting increased from Period 1 through 3. Examples of this pattern included fighting, swaying gait displays, naso-gential testing, courting and copulation. Nevertheless, differences between mean percentages for fighting were not significant whereas those for swaying gait displays and naso-genital testing were significant only for comparison between Periods 1 and 3. Differences were significant for comparisons between both Periods 1 and 3 and 2 and 3 for courting and copulation.

A second pattern consisted of mean values that decreased with time from Period 1 through Period 3. Changes in mean percentages suggested this pattern for smelling urine/flehmen but differences were not significant.

Croaking and bush thrashing composed a third pattern wherein mean percentages peaked in Period 2, but significant differences occurred for each behavior only for comparisons between Periods 1 and 2. A fourth pattern in which the behavior decreased in occurrence in Period 2 but increased again in Period 3 was suggested by the mean percentages associated with feeding, but no comparisons were significantly different. Our observations of dominant bulls indicated that feeding was nearly absent during 7-25 September with bulls beginning to feed again during the peak of the rut but not with great intensity.

Group Size and Composition

We determined group size and composition of rutting aggregations for 317, 532, and 361 individual moose for Periods 1, 2, and 3,

Table 4. Comparison of changes in time allocated to certain rutting behaviors by dominant bull moose during early, middle, and late stages of the rut in Denali National Park, Alaska, 1982-83. Numbers in the body of the table are mean percentages of time that bulls allocated to each behavior during all observation periods. Significant differences ($P < 0.05$) are indicated by letters in the body of the table.

Behavior	Mean % Time Allocated to Each Behavior		
	Period 1[1]	Period 2	Period 3
Feeding	19.1	1.9	7.5
Swaying gait	0.1A	1.4AB	2.6B
Bush thrashing	2.5A	4.4B	2.7AB
Croaking	7.9A	24.2B	20.5AB
Naso-genital testing	0.7A	2.9AB	5.8B
Smell urine/Flehmen	2.3	1.8	1.1
Courting/Copulation[2]	0.04A	0.04A	1.6B
Fighting[3]	—	0.04	2.3

[1] Period 1 = August 25-September 10, Period 2 = September 11-25, Period 3 = September 26-October 8.

[2] Courting = Chinning, attempted chinning, and mounting.

[3] Fighting = Lateral antler displays, antler clashes, and various combinations of goring.

respectively, of the rut during 1982 and 1983. Certain individuals, including radiocollared animals, were observed repeatedly during all 3 periods while others were seen only once. Moose were highly aggregated in the study area; between 95 and 97 percent of the individual moose observed during the 3 periods of the rut were associated with one or more other moose.

Aggregations of moose observed during the rutting period were classified as mixed groups (bulls, cows, and calves); bull groups (only bulls); cow groups (only cows); and cow-calf groups (only cows with calves) (Table 5). Mixed groups were by far the most common; groups containing only bulls, only cows, or only cows with calves were relatively rare. No significant differences occurred in the overall distribution of groups among the 3 periods of the rut ($\chi^2 = 8.21$, $P > 0.1$). Among the 4 kinds of groups, only cow-calf groups in the Period 1 versus Period 3 comparison had a significantly different frequency of occurrence ($\chi^2 = 4.87$, $P < 0.05$) when compared with all other groups combined. This was likely due to the timing of estrus in cows (Period 3) and the tendency of cows with calves to enter rutting aggregations during the peak of the rut.

Rutting aggregations were smaller during Period 1 than during Periods 2 and 3; median group sizes were 4, 6, and 7, respectively ($\chi^2 = 10.24$, $P < 0.01$) (Table 6). The upper range of group sizes was as large in Period 1 as it was in Period 3, however, indicating the tendency of moose in our study area to form large aggregations as early as late August.

Although as many as five Class 3 bulls occurred in some aggregations, the median number of such bulls was one for all 3 periods of the rut (Table 6). The median number of smaller bulls was also one with the exception of Period 2 in which over half the groups contained no smaller bulls. The median number of cows in mixed groups increased from Period 1(2) to Period 2(5) and then stabilized ($\chi^2 = 12.86$, $P < 0.01$). This accounted for the increase in median total group size.

Occurrence of calves in mixed groups increased markedly in Period 3 ($\chi^2 = 12.44$, $P < 0.01$) (Table 6). This correlates well with the decreasing occurrence of cow-calf groups in Period 3 (Table 5) and again indicates the tendency of cows with calves to join rutting aggregations as the peak of estrus approached.

To further clarify size of rutting

Table 5. Occurrence of four different types of moose groups observed during three different periods of the rut in Denali National Park, Alaska, 1982-83. No significant differences were detected in the overall distribution of groups.

		Percent of Total Groups in Each Period			
Period[1]	*n*	Mixed Groups	Bull-only Groups	Cow-only Groups	Cow/calf Groups
1	60	68.3	8.3	8.3	15.0
2	68	77.9	2.9	8.8	10.3
3	45	84.4	2.2	11.1	2.2

[1] Period 1 = August 15-September 10, Period 2 = September 11-25, Period 3 = September 26-October 8.

Table 6. Group size and composition of moose observed during three different periods of the rut in Denali National Park, Alaska, 1982-83. Groups containing only bulls, only cows, or only cows and calves were excluded.

				Group Composition							
		Total Group Size		Yearlings, Class 1 and 2 bulls		Class 3 Bulls		Cows		% of groups with calves	% of groups with ≥ 1 Class 3 bull
Period[1]	*n*	Median	Range	Median	Range	Median	Range	Median	Range		
1	41	4	2-23	1	0-4	1	0-4	2	1-22	2.4	75.6
2	53	6	2-37	0	0-7	1	0-3	5	1-22	7.5	86.8
3	38	7	2-23	1	0-8	1	0-5	5.5	1-21	26.3	84.2

[1] Period 1 = August 25-September 10, Period 2 = September 11-25, Period 3 = September 26-October 8.
[2] Size classes of bulls: yearlings had spikes, forks, or very small palmate antlers, class 1 bulls = antlers larger than yearlings but antler spreads less than 100 cm, class 2 = spreads 100-155 cm, class 3 = spreads more than 155 cm.

aggregations we divided mixed groups into six categories of size and determined the number of individual moose observed in each category during the three periods of the rut. Individuals infrequently aggregated into groups of two moose but individuals in groups of 3-7 were relatively common during all three periods of the rut (Table 7). About 25 percent of all individuals seen in Period 2 were in very large groups of 23 or more moose. The overall distribution of individuals among group size categories was significantly different ($\chi^2 = 145.6$, $P < 0.01$) for each period of the rut, but a relatively constant proportion (45-50%) of individuals occurred in large groups (13 or more moose) during each period.

DISCUSSION

Our data on classification and description of moose rutting behavior complements and, in some instances, augments descriptions provided by other authors including Dodds (1958), Altmann (1959), Geist (1963), and Lent (1974). In addition, we provide the first quantitative data on frequency, duration, and total time allocated to specific rutting behaviors.

We failed to observe particular specific behavioral acts described for moose in other areas of North America. For example, Altmann (1959) working in Wyoming described the initiator of a swaying gait display as usually circling around the recipient. Our observations indicated no circling associated with this display; participants approached each other and either initiated other displays, fought, or one animal departed without further escalation. Similarly, we observed no lateral approach as described by Altmann (1959) and Lent (1974) wherein a bull moves with a cow parallel to her and may stand sideways for prolonged periods close to the cow. Lent (1974) indicated that while walking with cows, bulls frequently use a swaying gait. We saw no evidence of this, nor did we recognize lateral approaches or what Altmann (1959) termed "driving." Such discrepancies may reflect varying behavior of moose in different geographical areas and may result from differences in group size and breeding systems characteristic of different areas.

The functional significance of behaviors also may vary geographically. Altmann (1959) interpreted the female moan as a loud, plaintive call for the bull and wrote of cows

Table 7. Occurrence of individual moose observed in six categories of group size during three different periods of the rut in Denali National Park, Alaska, 1982-83. Groups containing only bulls, only cows, or only cows and calves were excluded. The overall distribution was significantly different ($P< 0.01$).

Group Size	Period 1[1]		Period 2		Period 3	
	n	%	*n*	%	*n*	%
2	20	7.8	6	1.3	8	2.4
3-7	90	35.2	129	27.7	92	27.6
8-12	19	7.4	123	26.4	70	21.0
13-17	47	18.4	72	15.5	72	21.6
18-22	57	22.3	21	4.5	58	17.4
23+	23	8.9	115	24.7	33	9.9
Totals	256		466		333	

[1] Period 1 = August 25-September 10, Period 2 = September 11-25, Period 3 = September 26-October 8.

searching for bulls. Lent (1974) observed that cows may attract bulls with vocalizations but then act in a nonreceptive fashion. Our interpretation of the female moan is that it frequently is uttered in protest to courtship behavior by bulls and its frequency increases as yearling bulls or smaller satellite bulls persist in harassing cows. We do not consider the female moan to be a "mating call" initiated by cows to attract bulls, but we acknowledge that bulls may be readily attracted by it.

Although Lent (1974) stated that appeasement whines of bulls are apparently not produced after the second year, we observed older bulls emit this vocalization. Even dominant, Class 3 bulls will whine if they are displaced by a rival male and are subsequently threatened, or if they lose a fight, suffer injuries, and persist in the area occupied by the victorious bull.

Wallowing and the digging of rutting pits have long been known to characterize behavior of moose during the breeding season (Tanton 1920, Thompson 1949, Woodin 1956). More recent observations (Bubenik 1983, Miquelle and Van Ballenberghe 1985, Miquelle 1991) have provided additional details on behaviors associated with wallowing and its functional significance in moose. Our observations indicate that wallowing is initiated by bulls of all ages and occurs frequently during all stages of the rut. We observed that pits are dug by bulls where they happen to be, rather than in response to female urine or to the presence of other pits. Cows frequently become alert as bulls begin to dig a pit but do not approach the pit until the bull urinates. We have not observed bulls to urinate several times during a single wallowing sequence as reported by Geist (1963) and de Vos *et al.* (1967), but rather to attempt urination several times before succeeding. Splashing is performed immediately following urination; both sexes use identical motor patterns when splashing. Cows may try to displace the bull from the pit even before urination is complete. If several cows are present, vigorous competition may occur between them for the right to wallow; a winner's tenure in the pit may be brief as other cows vigorously try to displace her.

Although cows are strongly attracted to a bull's urine, and the wallowing process is an important component of rutting behavior and appears to influence an individual's breeding success, we have observed bulls vigorously defending their wallows against intrusion by cows. We have no explanation for this behavior.

Data on group size and rutting aggregations generally reflected changes in the aggregation patterns of individuals as the rut progressed. Our data and observations from other years (Van Ballenberghe and Miquelle, unpublished) combined with data presented here indicate that bulls aggregate mainly with each other early in the rutting period. This is especially true for Class 3 bulls; Class 1 bulls, and especially Class 2 bulls, may search more actively for cows and aggressively herd and court them during early stages (Period 1) of the rut. During the middle (Period 2) stage of the rut, however, Class 3 bulls associate more with cows and become dominant bulls in large mixed groups well before cows reach the peak of estrus. Changes in median group size during Period 2 were due largely to the tendency of cows to form larger groups during this period than during Period 1 (Table 6). We defined the peak of the rut (period 3) based on the frequency of copulation (Van Ballenberghe and Miquelle 1993); the latter behavior was totally absent in Periods 1 and 2. Cows with calves were significantly associated with rutting aggregations only during Period 3 (Table 6).

Our observations suggest that moose in DNPP have a highly polygynous breeding system with the most dominant bulls responsible for the majority of the copulations (Van Ballenberghe and Miquelle 1993). Moose in many parts of the world are considered to be serially monogamous (Markgren 1974, Bubenik 1985). Altmann's (1959) early descriptions of driving and the formation of tending bonds provided the only published clues to the mating system of moose until recently. Although we have seen tending bonds involving one bull and one cow, this is rare in DNPP; most of the observed mating occurred in rutting aggregations. These may contain up to 40 individuals and are mobile, unstable groups of cows, one dominant bull and often several satellite bulls unable to defeat the dominant bull. Fighting is common as is turnover of dominant bulls. Peek *et al.* (1986) analyzed interactions between size classes of bulls in our study area and documented the presence of a dominance hierarchy with the largest bulls acquiring the top rank.

Although dominant bulls defend rutting aggregations, and threaten and herd cows, moose do not form harems. We concur with Lent (1974) that bull moose do not bring females together or significantly control their movements as do males of species that form true harems. Although on occasion bulls attempt to direct cow movements, in general bull moose cannot prevent cows from leaving or joining aggregations and cows determine the direction and rate of travel of the group. Courtship and mating take place within the group. Thus, the mating system is intermediate between a true harem system and a tending bond system, similar to that described for desert mule deer (*Odocoileus hemionus crooki*) by Kucera (1978).

Several ecological factors contribute to the type of mating system observed for moose in DNPP, and perhaps in general in northern latitudes. Habitat in mountainous areas and near treeline is relatively open and animals can readily observe each other from afar. Periodic harsh winters and differential predation on the sexes both contribute to a highly skewed adult sex ratio; in recent years the Denali adult moose population has been about 70 percent female despite total prohibition of hunting. Mortality of calves, primarily caused by predation, resulted in about 90 percent of adult females being barren during the rut.

This facilitates formation of groups; cows with calves are notoriously antisocial and aggregate with other moose only to mate (Miquelle *et al.* 1992, Molvar and Bowyer 1994). Densities of moose also may be very low in northern areas where plant communities dominated by coniferous tree overstories result in habitats of low carrying capacity for moose. Taken together, these factors encourage formation of aggregations and discourage pair bonds involving only two moose.

Our data on time allocated to various behaviors indicate that bulls spend a disproportionate amount of time on social behavior during the rutting period. Although data on lone bulls and satellite bulls in mixed groups present only a crude picture due to small sample sizes, social behavior occupied 37% and 54%, respectively, of the total time bulls in these two categories were active (Table 2). Social behavior of lone bulls reflects instances where bulls were predominantly alone during observation periods but aggregated with other moose during segments of some periods. Bulls in bull-only groups spent 60% of their time in social behavior, while dominant bulls in mixed groups engaged in social behavior 44% of the time. Bulls that are dominant late in the rut often aggregate in bull-only groups early in the rut suggesting that bulls engage in high levels of social behavior throughout the entire rutting period.

Certain social behaviors are energetically costly and may involve risk of serious injury or death. Dominant bulls must defend cows by chasing satellites and fighting challengers. Feeding and energy intake of dominant bulls cease early in the rut and do not resume until late September (Miquelle 1990). Satellite bulls, especially yearlings and class-one bulls, feed throughout the rutting period and thereby reduce the stress of the rut.

Cows, in contrast to bulls, spent only 12% of their time in social behavior (Table 1). Cows continued to feed at high intensity throughout the rutting period. Cows apparently invest a much smaller amount of time, and probably energy, in the rut. Serious aggression among cows occurs only during attempts to gain access to rutting pits, an activity with a low probability of injury.

Estimates of the true cost of rutting for cows are likely higher than simply the amount of time spent in social behavior. Alert behavior and standing are likely higher than during other seasons as a result of the many interactions occurring in rutting aggregations. In addition, cows are commonly disturbed from resting periods by the approach of both satellite bulls and dominant bulls eager to test and court them.

ACKNOWLEDGMENTS

We gratefully acknowledge the field assistance of V. Schlotter and P. Butteri, data compilation and typing by K. Wenzlick and L. Patton, and the cooperation and assistance of the U.S. National Park Service in allowing us to conduct research in DNPP.

REFERENCES

ALTMANN, M. 1959. Group dynamics in Wyoming moose during the rutting season. J. Mamm. 40:420-424.

BARRETTE, C. and D. VANDAL. 1986. Social rank, dominance, antler size, and access to food in snow-bound wild woodland caribou. Behaviour 97:118-146.

BOWYER, R.T., V. VAN BALLENBERGHE, and K.R. ROCK. 1994. Scent marking by Alaskan moose: characteristics and spatial distribution of rubbed trees. Can. J. Zool. 72:2186-2192.

BUBENIK, A. B. 1983. Behavioral significance of the moose bell. Alces 19:238-245.

_____. 1985. Reproductive strategies in cervids. Pages 367-373 *in* P. F. Fennessy and K. R. Drew, (eds.) Biology of deer production. Royal Society of New Zealand Bulletin 22.

de VOS, A., P. BROKX and V. GEIST. 1967. A review of social behavior of the North American cervids during the reproductive period. Am. Midl. Nat. 77:390-417.

DODDS, D. G. 1958. Observations on prerutting behavior in Newfoundland moose. J. Mamm. 39:412-416.

FAGEN, R. M. and R. N. GOLDMAN. 1977. Behavioural catalogue analysis methods. Anim. Behav. 25:261-274.

GEIST, V. 1963. On the behaviour of North American moose (*Alces alces andersoni* Peterson 1950) in British Columbia. Behaviour 20:377-416.

KUCERA, T. E. 1978. Social behavior and breeding system of the desert mule deer. J. Mamm. 59:463-476.

LEHNER, P. N. 1979. Handbook of ethological methods. Garland STPM Press, New York. 403pp.

LENT, P. C. 1974. A review of rutting behavior in moose. Naturaliste can. 101:307-323.

MARKGREN, G. 1974. The question of polygamy at an unbalanced sex ratio in moose. Pages 756-758 *in* V. Geist and F. Walther, (eds.) Behaviour of ungulates and its relation to management. International Union for the Conservation of Nature, Morges, Switzerland.

MARTIN, P. and P. BATESON. 1986. Measuring behavior: an introductory guide. Cambridge University Press, Cambridge, G.B. 200pp.

MIQUELLE, D. G. 1990. Why don't bull moose eat during the rut? Behav. Ecol. Sociobiol. 27:145-151.

_____. 1991. Are moose mice? The function of scent-urination in moose. Am. Nat. 138:460-477.

_____. and V. VAN BALLENBERGHE. 1985. The moose bell: a visual or olfactory communicator? Alces 21:191-213.

_____, J. M. PEEK, and V. VAN BALLENBERGHE. 1992. Sexual segregation in Alaskan moose. Wildl. Monogr. 122. 57pp.

MOLVAR, E. M. and R. T. BOWYER. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. J. Mamm. 75:621-630.

PEEK, J. M., V. VAN BALLENBERGHE, and D. G. MIQUELLE. 1986. Intensity of interactions between rutting bull moose in central Alaska. J. Mamm. 67:423-426.

RISENHOOVER, K. L. 1986. Winter activity patterns of moose in central Alaska. J.Wildl. Manage. 50:727-734.

TANTON, T. L. 1920. Depressions found on moose trails and their significance. J. Mamm. 1:142-143.

THOMPSON, W. K. 1949. Observations of moose courting behavior. J. Wildl. Manage. 13:313.

VAN BALLENBERGHE, V. 1982. Growth and development of moose antlers in Alaska. Pages 37-48 *in* R. D. Brown, ed. Antler development in cervidae. Caesar Kleberg Wildlife Research Institute, Kingsville, Texas.

_____ and D. G. MIQUELLE. 1990. Activity of moose during summer in interior Alaska. J. Wildl. Manage. 54:391-396.

_____ and _____. 1993. Mating in moose: timing, behavior, and male access patterns. Can. J. Zool. 71:1687-1690.

WALTHER, F. R. 1984. Communication and expression in hoofed mammals. Indiana Univ. Press, Bloomington. 423 pp.

WOODIN, H. E. 1956. The appearance of a moose rutting ground. J. Mamm. 37:458-459.