SPRING MIGRATION OF FEMALE MOOSE IN CENTRAL SWEDEN

F. Sandegren and R. Bergström
Swedish Sportsmen's Association, Wildlife Research Unit, Box 7002, S-75007
Uppsala, Sweden

and

G. Cederlund and E. Dansie
Grimsö Research Station, S-77031 Riddarhyttan, Sweden

Abstract: Twelve female moose (*Alces alces*) were radio-collared and tracked from aircraft and from ground during the 1982 northward spring migration in central Sweden. Migration onset, speed and routes of migration, and daily activity pattern before during and following migration were studied. Onset of migration coincided with decreased snow cover and depth. All females began to migrate from April 14 to May 2. Distances moved varied from 14 - 60 km. The longer a distance to migrate the faster the females moved northwards. All females returned to summer home range used before. Females were more active in terms of movement during migration (35% of total time) than on winter (29%) and summer ranges (33%). Females spent more time in forward locomotion during migration (18%) then when on the winter range (9%). When on winter and summer home ranges, females were most active in the early morning and early evening hours. This pattern was less obvious during migration; however peaks of travelling did occur in early morning and early evening. Average distance moved/hour was significantly faster during migration (0.45 km) than on winter range (0.28 km; $P < 0.01$).

Moose migrations between seasonal home ranges are well documented in North America most frequently occuring in northern areas where moose have an opportunity to change elevation between summer and winter home ranges thereby optimizing their environment (Knowlton 1960, VanBallenberghe and Peek 1971, Le Resche 1974). However, few studies on moose migration have been made in Fennoscandia (Pulliainen 1974, Sandegren and Ahlqvist 1980).

Several studies have documented the traditional use of seasonal home ranges (Le Resche 1972, Phillips et al. 1973, Pulliainen 1974, VanBallenberghe 1977 and Ballard and Taylor 1980). Factors like snow, forage, social relations and their influence on moose movements have been discussed by Edwards and Ritcey (1956), Coady (1974), Hauge and Keith (1981), Knowlton (1960), Le Resche (1974), Phillips et al. (1973), Pulliainen (1974) and VanBallenberghe and Peek (1971). The complexity of factors that are and might influence moose movement patterns was discussed by Le Resche (1974).

This study, which is a minor part of a major study on moose migrations in Sweden was designed to get detailed information on the timing of spring migration in relation to changing snow conditions; to compare the onset and speed of migration among females with and without calves; and to compare daily activity patterns before, during, and after migration among females with and without calves.

STUDY AREA

The study area of 1359 km^2 is located 61-62^o N and 14.5-15.5^o E within the southern taiga zone (Fig. 1). Precambrian rocks and till dominate the geologic features. Sedimentary soils occur in lowlands.

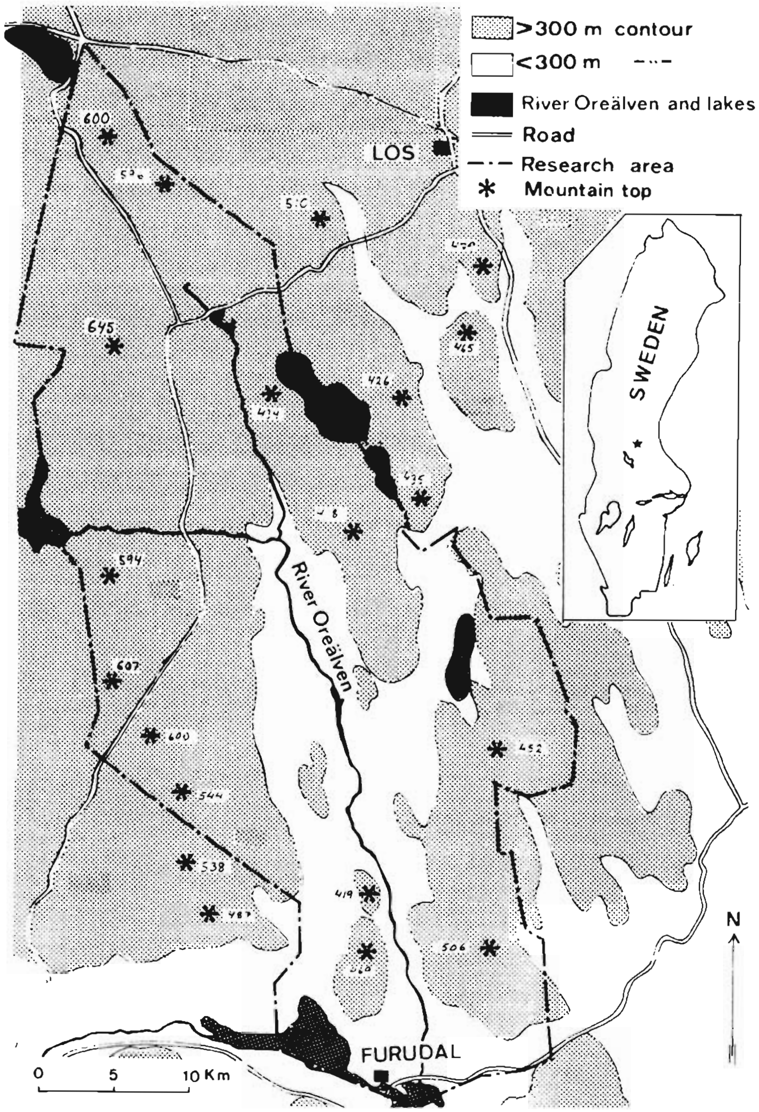

Fig. 1. Map of the study area and its location in Sweden.

The moose winter concentration area north of the village of Furudal and along the Oreälven river valley is at the 200 - 300 m elevation (lowland) whereas the upland summer range is at the 300 - 500 m elevation.

Climate is typical of the Swedish inland with mean temperatures in July and January of + 15^{o}C and - 7^{o}C, respectively. Mean duration of snow cover is 160 - 170 days in the southern lowland part and 2 - 3 weeks longer in the northern upland part (Pershagen 1969).

Pine (*Pinus silvestris*) and spruce (*Picea abies*) are the dominants in the tree layer where birches (*Betula pubescens* and *B. pendula*) are intermixed to a varying extent. These species are also the dominants in the shrub layer together with juniper (*Juniperus communis*), european mountain ash (*Sorbus aucuparia*) and willows (Salix spp). The field layer over most of the area is characterized by dwarf shrubs such as *Vaccinium myrtillus*, *V. vitis-idaêa* and *Calluna vulgaris*. In lowlands and especially on sedimentary soils lichens, predominantly Cladonia spp, are found.

Most of the land is owned by forest companies or the state. Forests are intensively managed with a highly variable clear cut size and a rotation period of 90 - 100 years. Clear cutting, followed by scarification and planting or natural regeneration, are ordinary practices. Clearing, thinning and fertilization are also common parts of the forest management.

Winter moose density in the study area since 1980 has averaged approximately 1/km^2 but up to 9 moose/km^2 in a 60 km^2 wintering area have been observed (Stålfelt pers. comm.). About 40% bulls were found in February 1982 when the population was counted.

In winter 1981-82 snow cover lasted from November 1 to May 19 at the upland northern stations and from November 11 to April 27 at the lowland southern stations. In late March, snow depth reached a maximum of 121 cm in the upland and 77 cm in lowland. This peak in snow depth was followed by a snow melt of approximately 3 cm/day until it disappeared. Snow depth in the upland was $\geq$ 70 cm for 60% of the time of snow cover compared with 3% in the lowland (Fig. 2).

METHODS

Field work was done from April 14 to May 18, 1982. Twelve radio-collared cows were followed, 5 with and 7 without calves (Table 1). Cow 09 split up with her female calf 77 when they were radiomarked in March 1982. All the cows were known to be migratory from previous studies. Aging was done by looking at tooth eruption and wear. Two age classes were distinguished (2 and 3+years). Cow 41 was accompanied by a yearling male throughout the study.

Females were radiotracked from ground and air. Ground tracking was done from a Volkswagen Van with an extendable and rotatable antenna through the roof (Cederlund et al. 1979). Most tracking was done from a Cessna 172.

Locations from the air were made twice a day on all the females from April 19 to May 16. While on the winter range additional locations of 9 females were taken every 2 hours from the ground during different 6 hour periods over 5 consecutive days to get equal coverage of the 24 hour period. Once females started migrating, individual cows were located hourly during different 8 hour periods over 5 days to cover the whole 24 hours.

A Gould Brush 220 two-channel analogue recorder was used to record the activity patterns. As the study began, the recorder was located on

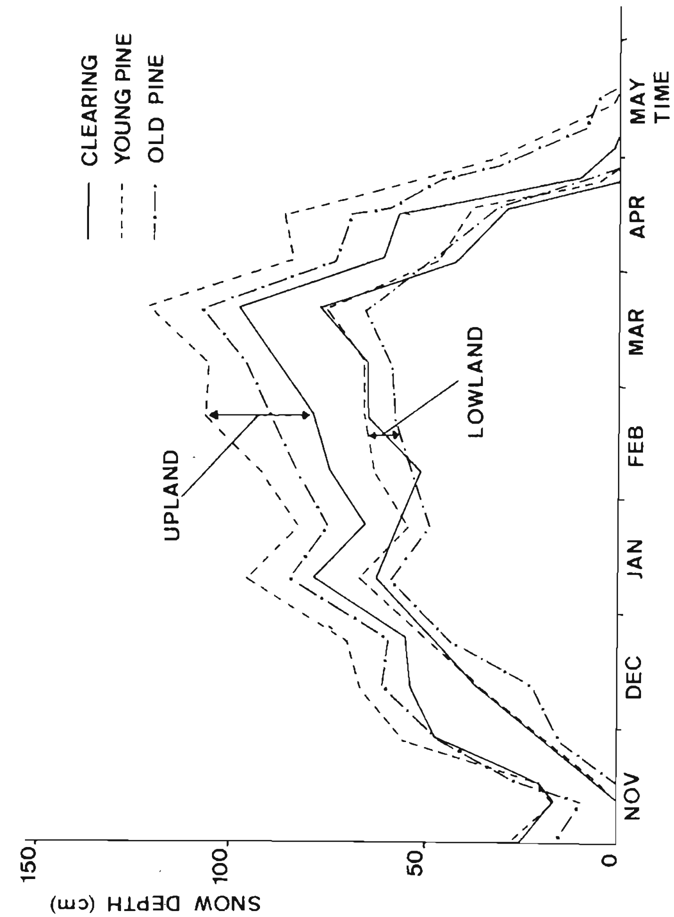

Fig. 2. Snowdepth in three different lowland and upland cover types during winter 1981-82.

TABLE 1. Date of onset of spring migration, date of arrival at summer range, straight line distance travelled and migration speed among 12 moose cows in the Furudal study area in 1982.

Moose	Age (years)	Calf	Onset (date)	Arrival (date)	Time taken (days)	Straight line dist. (km)	Speed of migr. (km/day)
09	8	0	23 Apr - 24 "	02 May - 03 "	9	14	1.5
10	8	2 ♀	02 May - 03 "	12 May - 14 "	11	30	2.7
12	9	1 ♂	28 Apr - 29 "	20 May	22	55	2.5
17	6	1 ♀	30 Apr - 02 May	20 May	20	27	1.4
29	6	0	24 Apr	09 May	15	55	3.5
32	8	0	14 Apr - 16 "	02 May	18	30	1.6
35	5	1 ♂	24 Apr	14 May	20	60	3.0
39	6	1	30 Apr - 02 May	16 May	16	55	3.4
41	8	0	25 Apr	20 May	25	57	2.3
47	2	0	16 Apr - 18 "	30 Apr - 02 May	14	40	2.9
48	2	0	25 Apr - 27 "	12 May - 14 "	18	55	3.0
49	2	0	23 Apr	10 May	17	32	1.8

the winter range. Once the females began to migrate the recorder was moved 30 km north.

From the activity recordings, we could distinguish active and non-active periods and within the active periods bouts with forward locomotion could be distinguished (Cederlund and Lemnell 1980).

The snow depth was measured throughout the period of snow cover at 10 different sites within the study area. Four stations were located on the lowland winter range. At each station, snow depth was measured from 30 permanent sticks, 10 in each of 3 different cover types: clearing, young and old pine stands (Fig. 2). Measurements were made every 2 weeks at each station over the whole winter. The frequency of taking measurements was increased to 2 times/week in the northern stations from April 1. In the wintering area, snow measurements were made daily from April 14 until the snow was gone. Percentage snow cover was estimated by counting the number of sticks registering 0 cm.

Students t-test, Chi-square and correlation analysis were used to compare data. Variation around means is expressed as standard deviation (SD). The P-level used was 0.01.

Migration is defined as a seasonal movement between geographically separated home ranges. Onset of migration is defined as the date after which the animal moved towards the summer range on 3 consequtive days. Time of arrival on summer range was defined as the date after which a female did not move further north or the day when she entered her previous summer range.

RESULTS

Winter Home Range

Just prior to migration onset some females moved quite long distances within and outside their previous winter home range. These "premigratory" movements were not necessarily directed towards the summer home range. Thus cow 29 made an undirected move of 4 km over a period of 24 hours just prior to migration. In 2 days, cow 17 rapidly moved 1.2 km east in the morning, 2 km west in the evening, and 2 km east again in the following morning. This happened about 6 days before she migrated north. These movements doubled her winter home range and brought her twice up to an elevation 100 m above her previous winter range.

Onset of Migration

All cows started to migrate between April 14 and May 3; 6 of them leaving April 23-26 (Table 1). We found no obvious connection between either female age and timing of migration or distance traveled and onset of migration.

Females without calves migrated 10 days before females with calves on the average. Between April 14-27 the seven calfless females began their migration, while one female with calf started on April 24, the others between April 28 - May 3 (Table 1).

Onset of migration coincided with rapidly decreasing snow cover in the wintering area (Fig. 3). When the migration started the snow depth on the winter range was well below the 70 cm level, which is considered

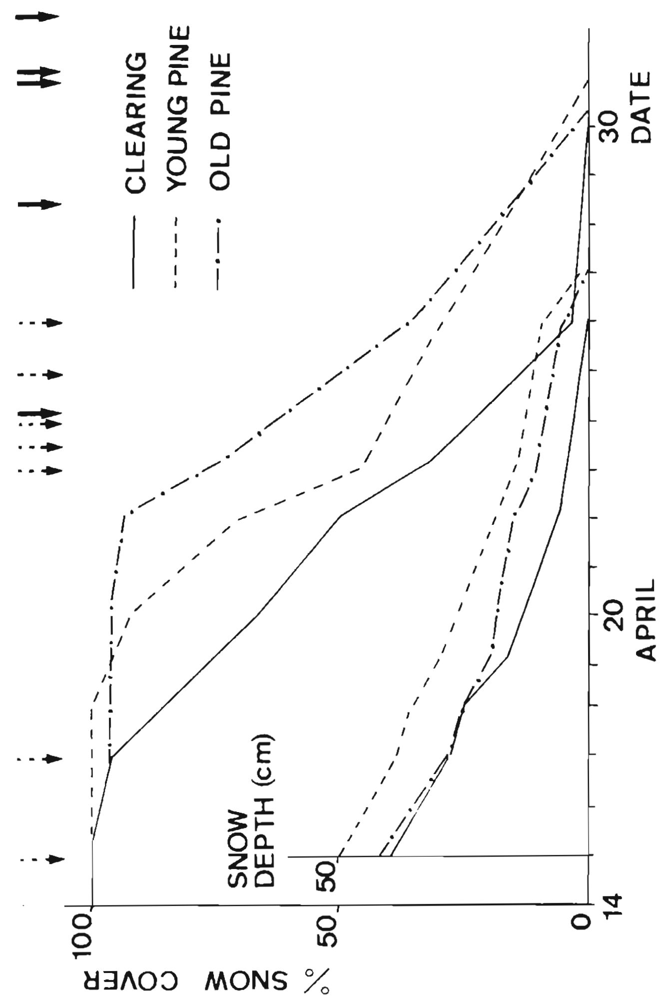

Fig. 3. Onset of moose migration in relation to snow cover and snow depth in three cover types. Arrows indicate time for onset of each cow (single cow; cow with calf at heel).

critical to moose (Coady 1974). Onset of migration did, however, coincide with the period when the snow depth in the upland rapidly went below the critical level (Fig. 2). In 1980, most cows left between April 14 and 26 (Sandegren unpubl.).

Migration Routes

Ten migrating cows moved north in the Oreälven river valley up to their upland summer ranges. The distances migrated varying from 14 to 60 km. Cow 12 moved 55 km NE and cow 17 moved 27 km NW to their summer ranges (Fig. 4).

Dirt roads running north along the river were heavily used by migrating moose. Cow 41 was followed on a dirt road for 65 minutes while she covered 1.2 km. She walked slowly now and then leaving the road to browse. Similarly, cow 10 and her twin calves were observed migrating along the road. They were also observed near the road on several occassions. Also well defined paths in swamps were used by many moose. Thus most migrating moose in the study area appear to use a few well defined and easily walked routes during spring migration.

Speed of Migration

Cow 47 moved 9 km in 40 hours, with a maximum speed of 1.2 km/hour while cow 49 once moved 1.9 km in one hour which was the longest distance recorded between hourly locations. Moves of 1 km/hour or more were however uncommon. The females that we followed were only moving longer than 1 km in 9% of the cases when the distances between hourly locations were obtained.

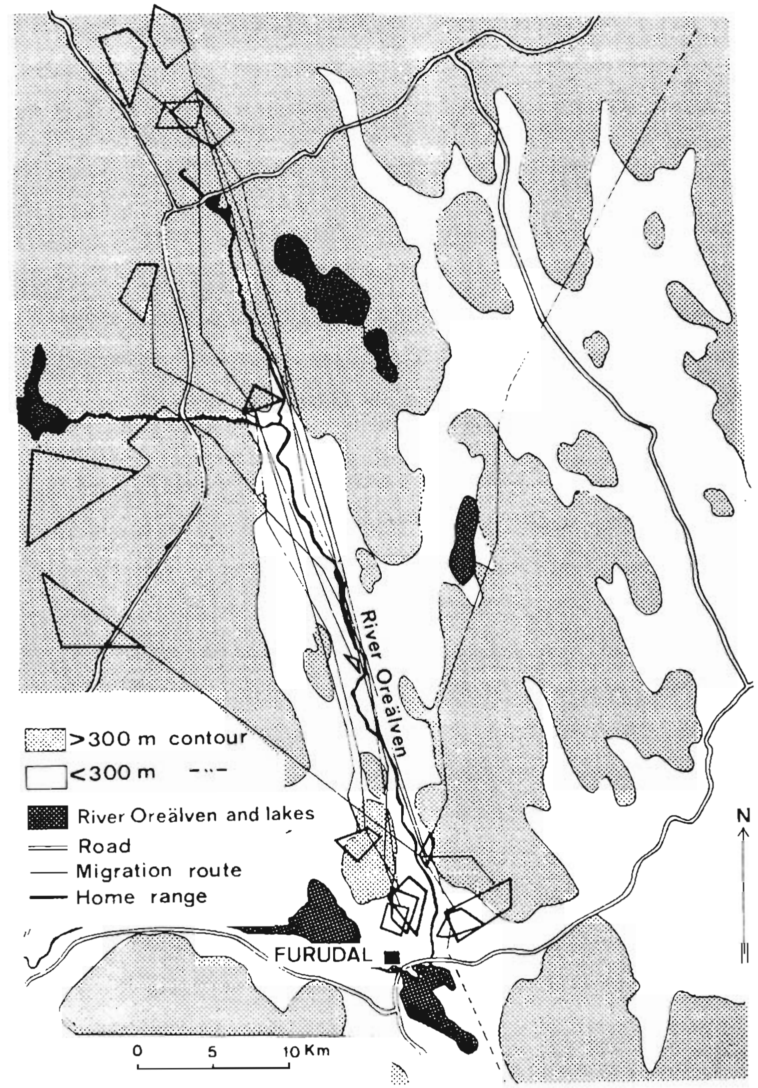

Fig. 4. Spring migration routes and seasonal home ranges of moose cows moving along the Oreälven river valley in 1982.

The distance travelled per day varied greatly and sometimes cows stopped for 1 - 3 days. Cow 41 was followed closely on May 10-11 and May 15-16. On May 10-11 she did not move north at all, but on May 15-16 she moved 11.5 km, covering 5.3 km each day. Cow 10 covered distances of 6.5, 3 and 1 km on three following days (Fig. 5).

Mean straight line distance between locations taken at 4 hour intervals was longer among migrating females (1.06 km) than among females on the winter range (0,56 km, $P < 0.01$, Table 2). Distances travelled also varied throughout the day with peaks at sunrise and late afternoon among females on the winter range and migrating (Table 2). Distances were longer among migrating females at all times of the day ($P < 0.01$) except at sunrise and late afternoon. Similarly the mean straight line distance between hourly locations among active migrating females was longer (0.45 ± 0.3 km) than among active females on the winter range (0.28 ± 0.14 km, $P < 0.01$).

Arrival at Summer Range

All but three cows were on their summer ranges by May 16. Cow 47 that first arrived came between April 30 and May 2. The majority of the cows arrived between May 9 and May 16. Cows 12, 17 and 41 had not reached their summer ranges by May 16 although cow 12 was spotted 4 km south of her summer range on May 20 (Table 1). They subsequently arrived before calving.

The first 3 cows to arrive at their summer ranges (09, 32 and 47) all moved north of their summer ranges before moving back into them. This "loop" approach has also been observed in previous years.

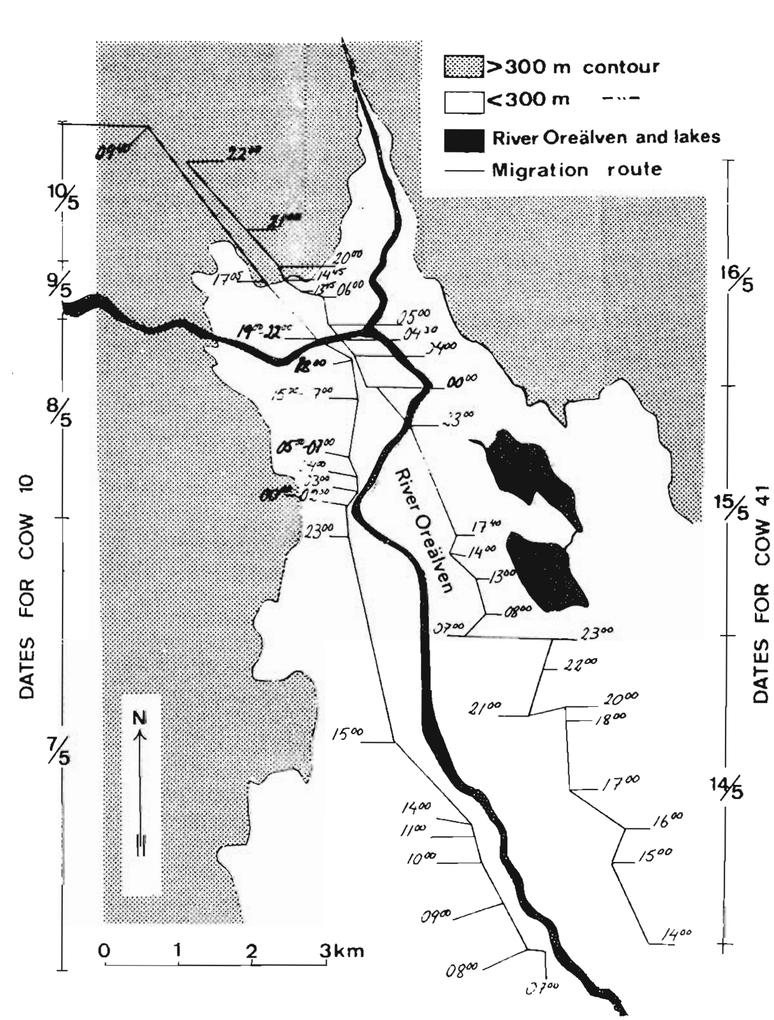

Fig. 5. Detailed migration routes of moose cow 10 and cow 41 along the Oreälven river valley in May 1982. Date and hour of each location is indicated.

TABLE 2. Straight line distances moved during 4 hour periods for female moose migrating and on winter home range.

Time interval	Winter range $\bar{X} \pm SD$	N	Migration $\bar{X} \pm SD$	N
23.00 - 03.00 nighttime	0.2 ± 0.22	7	0.53 ± 0.30 [a)]	8
03.00 - 07.00 sunrise	0.95 ± 0.29	8	1.58 ± 1.20	8
07.00 - 11.00 daytime	0.38 ± 0.29	8	0.77 ± 0.59 [a)]	8
11.00 - 15.00 "	0.44 ± 0.31	7	1.09 ± 0.60 [a)]	8
15.00 - 19.00 "	0.94 ± 0.41	8	1.24 ± 0.78	9
19.00 - 23.00 sunset	0.36 ± 0.30	8	1.08 ± 0.94 [a)]	9
MEAN OVER 24 HOURS	0.56 ± 0.42	46	1.06 ± 0.84 [a)]	50

[a)] Significant difference ($P < 0.01$) between winter range and migration.

Straight Line Distance travelled during Migration

Straight line distances between the last location prior to the onset of migration to the first location on the summer range were 14 - 60 km with a mean of 42 km (Table 1). The average move towards the summer range varied from 1.4 - 3.4 km/day with a mean of 2.5 km/day (Table 1). We found a significant positive correlation between the straight line distance travelled and the velocity among individual cows (Fig. 7).

Acitvity Patterns

Activity patterns were obtained during 361, 314 and 77 hours for females on the winter home ranges, during migration and on summer home ranges respectively.

Females were most active around sunrise and sunset on winter and summer home ranges. Active peaks were less distinct during migration, when activity was more evenly distributed over the 24 hours (Fig. 6). The mean time active was higher among migrating cows (35% of total time, N = 7) than females on winter range (29%, N = 5) or summer range (33%, N = 2).

The percentage of time in forward locomotion varied during the day; peaks in forward locomotion coincided with peaks in activity during winter, migration and summer. Mean time spent moving forward was higher during migration (18%) than during winter (9%) or summer (12%).

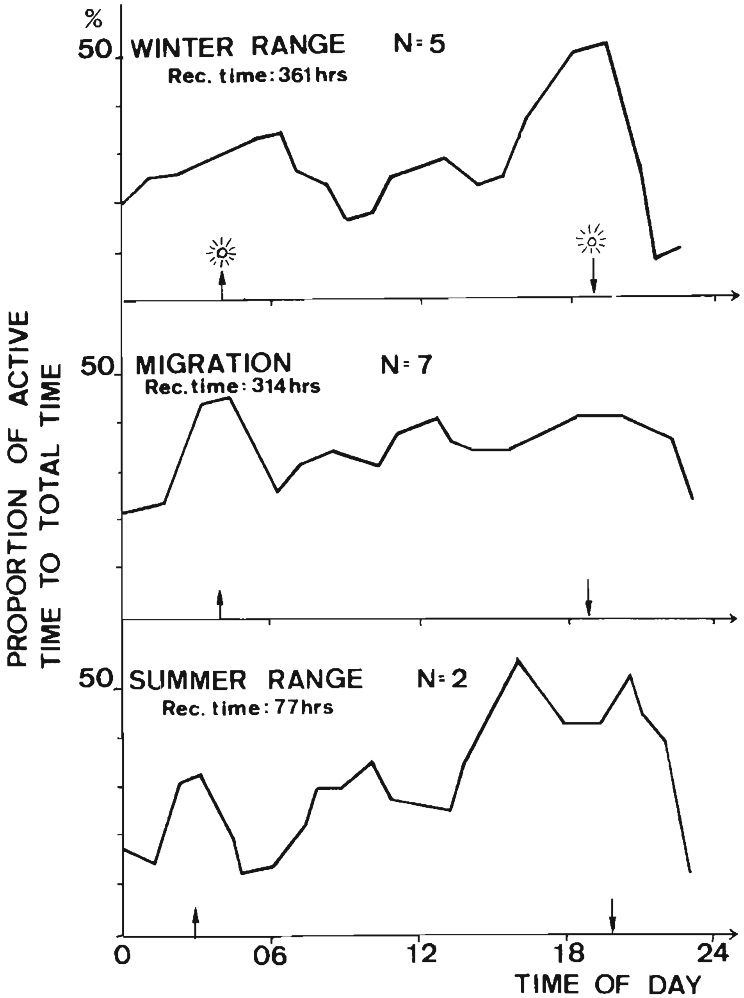

Fig. 6. Daily activity pattern of cow moose on the winter range, during migration, and in the summer.

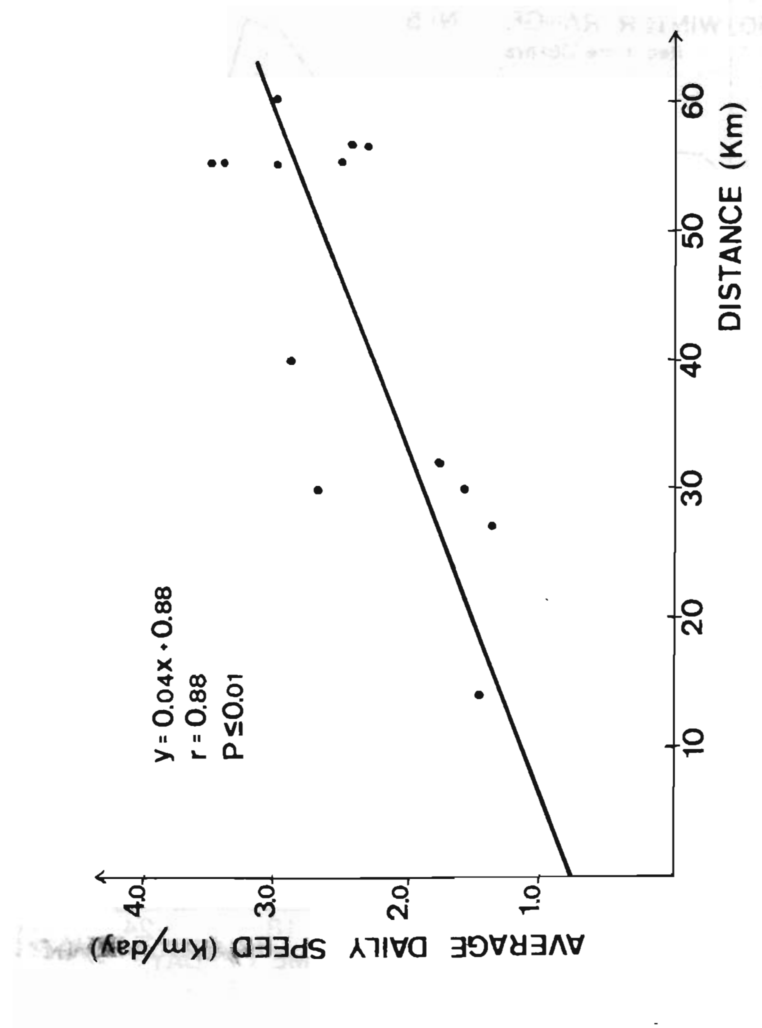

Fig. 7. Relation between distance of migration and daily speed of cow moose during spring 1982.

DISCUSSION

Movements, feeding and acitivity of moose are affected by the snow conditions (Formozov 1946, Nasimovitch 1955, Coady 1974). Snow depths > 70 cm may seriously restrict activities and cause moose to use more energy in locomotion than can be compensated for by feeding (Kelsall 1969, Ritcey 1967, Thomson and Vukelich 1981). In the highland of our study area, snow depths ≥ 70 cm lasted for about 120 days compared with about 12 days in lowland wintering area. Deep snow probably encouraged our cows to leave highlands in winter similar to moose in North America under similar conditions (Edwards 1956, Harry 1957, VanBallenberghe 1977).

Our study began in April when snow depth was rapidly decreasing on winter range. Thus, our animals might have been in a transitional stage between winter and migrating behaviour, i.e. in a premigratory mood.

Proximate factors suggested to trigger the migration in moose include temperature (Edwards and Ritcey 1956), snow depth (Formozov 1946, Hauge and Keith 1981, Nasimovitch 1955) and plant phenology (Knowlton 1960). Our animals stayed in winter home ranges until the ground was almost bare, i.e. long after snow would impede movements. Thus, snow depth did not prevent migration onset unless the females perceived the snow situation in the highland or knew from experience that snow persisted longer in the highlands. It is worth noting that: (1) several females made premigratory movements back and forth towards the highlands just prior to migrating; seemed to be testing the highland conditions, (2) adult females without calves migrated just as highland snow depth declined below 70 cm, the critical level to adult moose (Coady 1974), (3) females with calves left after lone females and just at the time when snow conditions became favourable to calf locomotion

in the highland. This behaviour could certainly be adaptive.

Phillips et al. (1973) compared spring movements of bulls and cows away from their winter ranges, the mean date of departure of bulls being one day later than for cows. VanBallenberghe (1977) suggested that date of parturition affected date of arrival of females on their summer ranges; some pregnant females migrating back to summer ranges immediately preceeding parturition, Roussel et al. (1975) found no difference in movement between cows with and without calves. Best et al. (1978) compared daily activity patterns of moose over the year and showed that animals moved most in the spring. But we have found no detailed information on the behaviour of moose in connection with the spring migration in the literature.

Onset of migration coincided with the first appearance of bare ground and the majority of the females left when the percentage of bare ground rapidly increased (Fig. 3). This suggests that availability of ground vegetation might have been an important triggering factor. Migrating females were observed to feed mainly on _Vaccinium myrtillus_ an important food species not available during winter but now available throughout the area as the snow left the ground. Hoskinson and Tester (1980) found that onset of migration among pronghorn antelopes (_Antilocarpa americana_) coincided with the break up of snow cover when animals were able to take advantage of additional forage, and Knowlton (1960) concluded that the "greening up" of forage initiates spring movements of moose.

In our study the spring migration may have been mediated both by the disappearance of snow and the changing availability of forage. Internal timing mechanisms that of course are influenced by external stimuli might also be involved. The fact that cow moose started to migrate in exactly the same period with a major peak in week 17 in both 1980 and 1982 certainly indicates that factors like day length, light intensity etc might be involved.

Various social factors could also be involved in onset of migration. The fact that cows without calves left first might be related to a more gregarious nature of this group while females with calves are more solitary (Mytton and Keith 1981, Peek el al. 1974). Single cows might have been "triggered" by cows in the viscinity whereas the more solitary cow-calf groups would not be influenced in this way. Also the cow with calf may be waiting until the condition of the calf enables it to take the hardships of a migration. Undoubtedly many calves have appeared to be in a poor physical condition in this crowded and overbrowsed area during recent years. This should be looked further into. Once migration started the speed of cow-calf groups did not deviate from the speed of single females.

Best et al. (1978), Geist (1960) and de Vos (1958) observed activity peaks around sunrise and sunset. Geist (op. cit.) also described a single activity peak in midday, which was accompanied by a second peak as daylight hours increased in the summer. In our study the sunrise and sunset peaks were obvious while the females were on winter- and summer home ranges and a third peak in midday was indicated. While migrating, the females were generally more active and lost the distinct diurnal activity pattern. This may be a result of an increased amount of forward locomotion within the activity periods making it necessary to extend the active periods over the whole day. Since peaks in forward locomotion coincided with peaks in general activity, it would seem that neither feeding nor locomotion are confined to specific times of day. Thus the migrating moose will take the opportunity to feed while on route, which

extends the active periods. Direct observations of females feeding while migrating further supports this idea.

Migration like other forms of adaptive behaviour, is a product of natural selection (Lack 1968). According to Lack (op. cit.), the advantages of migration and winter residency are roughly equal in partial migrants like the moose where some move seasonally and others are sedentary. The advantages of migration differ in different places, different years in the same place and in different age and sex groups.

According to Cox (1968), the primary selective agents in the evolution of migration among animals living in a seasonal environment are probably intra- and interspecific competition. If gains in survival or reproduction due to reduced competition exceed the cost of migration then evolution of migratory behaviour in a normally resident population should evolve.

ACKNOWLEDGEMENTS

We thank Per Ahlqvist, Lennart Pettersson, Olle Persson, Olle Jakobsson, Hardy Kareliusson and Uno Wallberg for their devoted work in the field and Kjell Larsson for his help with the data analysis.

The Swedish Sportsmen's Association and the National Swedish Environmental Protection Board have financed the project.

REFERENCES

BALLARD, W. B. and K. P. TAYLOR. 1980. Upper Susitna Valley moose population study. Alaska Dept. of Fish and Game. Final Rept. W-17-9, 10 and 11. 101 pp.

BEST, D. A., G. M. LYNCH, and O. J. RONGSTAD. 1978. Seasonal activity patterns of moose in the Swan Hills, Alberta. Proc. N. Am. Moose Conf. Workshop. 14: 109-125.

CEDERLUND, G., T. DREYFERT, and P. A. LEMNELL. 1979. Radio tracking techniques and the reliability of systems used for larger birds and mammals. National Swedish Environmental Protection Board, Stockholm, 1979. PM 1136: 1-102.

__________ and P. A. LEMNELL. 1980. Activity recordings of radio-tagged animals. Biotelemetry Patient Monit. 7: 206-214.

COADY, J. W. 1974. Influence of snow on behavior of moose. Nat. Can. (Que.). 101: 417-436.

COX, W. G. 1968. The role of competition in the evolution of migration. Evolution 22: 180-192.

EDWARDS, R. Y. 1956. Snow depths and ungulate abundance in the mountains of western Canada. J. Wildl. Manage. 20: 159-168.

__________ and R. W. RITCEY. 1956. The migrations of a moose herd. J. Mammal. 37: 486-494.

FORMOZOV, A. N. 1946. Snow cover as an integral factor of the environment and its importance in the ecology of mammals and birds. Transl. from Materials for Fauna and Flora of the USSR, New Series, Zoology 5 (xx) 1946: 1-152. Occ. Paper No. 1. Boreal Inst., Univ. of Alberta, Edmonton 141 p.

GEIST, V. 1960. Diurnal activity of moose. Mem. Soc. pro Fauna et Flora Fennica. 35: 95-100.

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. 45: 573-597.

HOSKINSON, R. L. and J. R. TESTER. 1980. Migration behaviour of pronghorn in southeastern Idaho. J. Wildl. Manage. 44: 132-144.

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

KNOWLTON, F. F. 1960. Food habits, movements and populations of moose in the Gravelly Mountains, Montana. J. Wildl. Manage. 24: 162-170.

LACK, D. 1968. Bird migration and natural selection. Oikos 19: 1-9.

LE RESCHE, R. E. 1972. Migrations and population mixing of moose on the Kenai Peninsula (Alaska). Proc. N. Am. Moose Conf. Workshop 8: 185-207.

__________ 1974. Moose migrations in North America. Nat. Can. (Que.). 101: 393-415.

MYTTON, W. R. and L. B. KEITH. 1981. Dynamics of moose populations near Rochester, Alberta, 1975-1978. Can. Field-Nat. 95: 35-49.

NASIMOVITCH, A. A. 1955. The role of the regime of snow cover in the life of ungulates in the USSR. Akad. Nauk SSSR, Moskva, 430 p. (Transl. from Russian, Can. Wildl. Serv., Ottawa.)

PEEK, J. M., R. E. LE RESCHE, and D. R. STEVENS. 1974. Dynamics of moose aggregations in Alaska, Minnesota and Montana. J. Mammal. 55: 126-137.

PERSHAGEN, H. 1969. Snötäcket i Sverige 1931-60. (Snow-cover in Sweden 1931-60). SMHI. Meddelanden. Serie A. Nr 5. (With English summary).

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

PULLIAINEN, E. 1974. Seasonal movements of moose in Europe. Nat. Can. (Que.). 101: 379-392.

RITCEY, R. W. 1967. Ecology of moose winter range in Wells Grey Park, British Columbia. Proc. Int. Workshop Moose Res. and Manage. Edmonton, Alberta. 15 p.

ROUSSEL, Y. E., E. AUDY, and F. POTVIN. 1975. Preliminary study of seasonal moose movements in Laurentides Provincial Park, Quebec. Can. Field-Nat. 89: 47-52.

THOMPSON, I. D., and M. F. VUKELICH. 1981, Use of logged habitats in winter by moose cows with calves in northeastern Ontario. Can. J. Zool. 59: 2103-2114.

SANDEGREN, F., and P, AHLQVIST. 1980. Älgens vandringar. Viltnytt 11: 2-9.

VanBALLENBERGHE, V. 1977. Migratory behaviour of moose in south-central Alaska. Trans. 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.

de VOS, A. 1958. Summer observations on moose behaviour in Ontario. J. Mammal. 39: 128-139.