A SYNOPSIS OF MOOSE MOVEMENT STUDIES IN FURUDAL, SWEDEN

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ABSTRACT: This paper summarizes the intergrated, multi-agency moose movement studies conducted at Furudal, in the southern inland taiga of Sweden, from 1980 to 1986. In this area high moose densities, combined with seasonal movements were resulting in management problems, primarily browse damage to pine forests in winter concentration areas. The Furudal population was partially migratory; ca. 70% engaged in seasonal return migrations. Individuals were consistently either migratory or non-migratory and independent offspring had the same migratory tendencies as their dams. Seasonal migrations occurred bianually. The mean onset of migration from summer to winter ranges varied from November 23 (1980), to January 25 (1983), and was correlated to a threshold snow depth of ca. 40 cm in summer-use regions. Mean onset of return migration to summer ranges was less temporally variable and occurred between April 18 and April 27 in all years. Migratory individuals used the same summer and winter areas yearly and no-return dispersal from summer and winter ranges was minimal (< 4% per yr). During winters with deep snow (> 70 cm), high densities of moose (> 11 moose/ km^2) in heavily-browsed pine forests formed temporary groups, had small winter home ranges (x=6.1 km^2) and exhibited intraspecific aggression. Cows utilizing this area had good recruitment of calves into the winter population (0.88 calves/cow/yr). During the study moose densities were high but decreasing, harvest rates were increasing, snow accumulation rates varied yearly, dispersal was low, migration onset varied and individual tendencies to migrate remained constant.

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Throughout much of Sweden moose populations are seasonally migratory.This adaptive behavior to exploit widely disjunct habitats enables moose to occur at greater abundances. The potential for high densities of moose e.g. 1-4 moose/km^2 over thousands of square kilometers in central Sweden (Cederlund *et al.* 1987, Cederlund and Markgren 1987), is partially attributable to the ability of moose to fully utilize available habitats through seasonal movements and to form winter concentrations, e.g., > 11 moose/ km^2 over thousands of hectares (Bergström *et al.* 1983, Sweanor and Sandegren 1989). However, the difficulty of predicting where large numbers of moose are going to be at any one time, as a result of seasonal migration, can cause critical misjudgements of population numbers and distribution, habitat utilization and forest damage, hunting pressure, and vehicular hazards.

The main objective of the Furudal migration studies was to describe the movements and distribution of moose in a typical high density, migratory population in central Sweden. Post-harvest numbers of moose in Sweden were increasing by almost 20% per year prior to these studies (Cederlund and Markgren 1987). Understanding movement patterns and the resultant changes in moose distributions was essential to managing migratory populations in Sweden.

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STUDY AREA AND METHODS

The area was in the southern taiga in central inland Sweden, located at approximately 61°N, 14.5°E. The study area, established in 1980 for baseline inventories of vegetation and population density, was 1359 km^2; however, some moose moved beyond the boundaries increasing the effective area of movement studies to ca. 4000 km^2 (Sweanor 1987). The area was typified by low, rolling hills, with elevations of 200 to 700m, interspersed with bogs. Forests consisted of pine (*Pinus sylvestris*) and spruce (*Picea abies*) mixed with birch (*Betula pubescens*, and *B. pendula*). The understory contained birch, willow (*Salix* spp.), common juniper (*Juniperus communis*), European mountain ash (*Sorbus aucuparia*) and *Vaccinium* spp. The forests were intensively managed for timber production and 75% of the region had harvest rotations of 90-100 years and contained clearcuts of 3-18 ha. Approximately 20% of the area was covered in forest stands less than ca. 20 years old. In an 1203 ha region of the study area, where moose concentrated during winter, 40% of young pine (< 20 years-old) had incurred from 5 to over 40% damage of their main stem from moose browsing (Bergström *et al.* 1983). The study area was described in more detail in Bergström *et al.* (1983) and Cederlund *et al.* (1987).

Field work was conducted from January 19, 1980 to October 25, 1986, with variable time periods for specific studies. Generally, moose were immobilized using 1.0-1.2 ml of a concentrated etorphine-xylazine mixture and were marked with ear tags and/or collars and/or radio transmitters using methods described in Sandegren *et al.* (1987). Movements of 140 moose (89F, 51M) were recorded through aerial and ground surveys and radio-tracking, behavorial observations and from hunter kill information. Moose densities were determined from aerial surveys. For the purpose of these studies migration was defined as seasonal return movements between spatially distinct winter and summer home ranges (see Sweanor 1987). Dispersal was defined as a no-return movement from an established home range (see Sweanor and Sandegren 1989). Movement patterns were defined as the combination of winter use area, summer use area and migration route (Sweanor and Sandegren in press). Methodologies and terminology for specific studies can be found in the referenced literature.

RESULTS

The moose population in the Furudal study area was partially migratory (Sweanor 1987). Approximately 70% of the marked population seasonally migrated ($x = 36.8 \pm 17.2$ km) between spatially exclusive winter and summer home ranges. The remaining 30% of the moose were nonmigrants and remained yearlong in regions occupied by migratory moose during either winter or summer. Migratory moose migrated to their winter ranges in late fall, some years, or early winter, other years, and returned to summer ranges in mid-spring. The migration of adult moose to their winter home ranges was not predictable from seasonal date, rather it was related to snow depth in summer-use areas. Mean onset of migration to winter ranges occurred at mean snow depths of ca. 40 cm (Sandegren *et al.* 1985). This snow depth is indicative of changes in the availability and quality of important foods such as dwarf shrubs (Cederlund *et al.* 1980 and Scharin 1980). When snow accumulations were delayed, moose migrations were also delayed. Migration of subadults (< 2 yrs-old) to winter ranges occurred earlier than adult migration. Migration to summer ranges consistently commenced in late April, an average of 5 ± 5.5 days before average snow depth was reduced to ca. 40 cm in summer-use areas.

The tendency of individuals to be migratory or nonmigratory was invariate during the study. None of the 140 marked moose changed from migratory to non-migratory behavior during 7 years of study. In addition, migrant versus non-migrant behavior was passed from mother to offsping. Thirteen migratory and 4 nonmigratory cows, respectively, produced 15 migratory and 6 nonmigratory offspring (Sweanor and Sandegren 1988). The migratory behavior of the offspring was determined when they were independent of their dam and had undergone at least 4 seasonal migration s.

Dispersal from the population was minimal and was not related to moose density which during summer was as high as 1.3 moose/ km^2 (Cederlund *et al.* 1987) and during winter, as high as 11.7 moose/km^2 (Sweanor and Sandegren 1989). Migratory moose used the same summer and winter home ranges year after year. Although calves physically separated from their dam during spring migration or early summer (Sandegren *et al.* 1982, Cederlund *et al.* 1987), as independent adults, they usually established summer as well as winter home ranges near or overlapping their dam's (Cederlund *et al.* 1987, Sweanor and Sandegren 1989).

Summer and winter home range sizes, determined as minimum convex polygons, not including migration routes, were highly variable. Mean summer home range size of cows was 7.4 ± 0.7 km^2(n=96). Summer home range size varied yearly but was independent of the cow's age (Cederlund *et al.* 1987). Winter home range size varied from 0.3 to 104.0 km^2 ($\bar{x}$=11.5 ± 13.9 km^2, n=183) Mean winter home range size was significantly different in winters with different durations of snow depth > 70 cm. During a winter with 7 weeks of snow depths greater than 70 cm, mean home range size (n=21) was only 6.1 ± 4.9 km^2. Winter home range size also tended to be reduced at high population densities, but was not correlated with the age or sex of moose (Sweanor and Sandegren 1989).

In winter concentration areas moose formed groups and exhibited intraspecific aggression at an average rate of one encounter every 5.5 hrs per moose associated with (Sweanor and Sandegren 1986, 1987). Cows with calves encountered the highest rate of aggression, one interaction every 2.5 hrs per moose associated with. Group formation was temporary, lasting from minutes to days, and averaged 3.4 ± 2.6 moose per group.

The movement patterns of winter and summer range use of individual moose remained stable during the study but recruitment success for cows using different movement patterns was different ($p< 0.05$, Sweanor and Sandegren in press, Sweanor 1987). For example, 35 cows using the main winter concentration area for 108 cow years had a recruitment rate of 0.88 calves/cow/year, whereas 13 cows wintering in an area north of the main winter concentration area for 34 cow years had a recruitment rate of 0.59 calves/ cow/year. Mortality rates of cows having different patterns were not different ($p=0.35$).

Discussion and Management Considerations

To manage moose, it is necessary to understand their movements. Movements of moose affect the eveness of the population distribution, the intensity of local habitat utilization and the potential for redistribution of the population. From a management point of view movements of greatest concern are migration and dispersal.

The Furudal moose population was dimorphic, consisting of migratory and nonmigratory segments. The proportion of migrants to nonmigrants appeared to be determined by their respective survival and reproductive success, since moose were consistently either migrants or nonmigrants, and offspring adopted the migratory behavior of their dams (Sweanor and Sandegren 1988). The timing of migration was related to a threshold snow depth of ca 40 cm, which is consistently surpassed in this region (Lillhamra meteorological station, Swedish Meteorological and Hydrological Inst., Norrköping, Sweden). The invariate migratory response of individual moose, the transmission of migratory response from cow to calf and the regularity of snow depth surpassing 40 cm appear to be catalysts resulting in the dimorphism of migrants and nonmigrants in this population.

Why some moose did not migrate in response to threshold snow depths is not known. Some nonmigratory moose were located on winter concentration areas year-round and had no need to migrate to avoid deep snows. Yet, other nonmigratory moose were located in regions occupied by migratory moose only during summer. These nonmigratory moose apparently did not respond to threshhold snow depths of 40 cm and never migrated to known winter ranges. This may indicate that some moose successfully overwinter, not only at snow depths that trigger migratory behavior in other moose but also at the subsequently deeper snows that follow threshhold levels. However, since snow measurements in this study were mean depths from random sample points and home range habitats of non-migratory moose were not intensively studied during winter, another plausable explanation is that non-migrants did, in fact, have access to winter habitat, comparable to that used by migratory moose, within their home range. Perhaps this habitat consisited of a series of microhabitats with reduced snow depths, e.g., wind swept slopes or dense forest stands. The offspring of these moose would not disperse and thus could also utilize this habitat with reduced snow depth. Yet, some migratory moose had ranges near or even overlapping those of nonmigratory moose, and had accesss to the same habitat that sustained the nonmigratory moose through winter. That moose in these situations still migrated would indicate that migratory moose had a strong learned or genetic predisposition to migrate. In this population migratory moose learned from their dams where to migrate and thereafter adhered to those traditional routes exhibiting very little tendency to disperse. Perhaps exploratory or dispersal tendencies of moose in this population were dampened because familiarity with a migration route and remaining within migration distance of a known winter range affected subsequent survival.

In a population of moose such as Furudal, it is not easy to identify the segment of a moose population which is migratory, unless their individual movements are followed, because migratory moose can occur in areas also populated by nonmigratory moose in both winter and summer. Therefore, control of one segment of the population over the other is difficult (Sweanor 1987). However, some management considerations are evident. Migration to winter ranges occurs earlier and results in heavier use of winter concentration areas and more browse damage in years when snow accumulates early to depths of over ca. 40 cm (Sandegren *et al.* 1985, Sweanor 1987). The period of greatest vehicular hazard, a serious public-safety consideration in Sweden where moose cross heavily travelled railway and roadway systems, varies from year to year depending on snow accumulation patterns. Surveys, completed at the same time every year in areas containing migratory moose, may not be comparable for population trend analysis because moose do not migrate at the same time every year (Sweanor 1987). Management problems caused by high density populations can not be expected to be solved by dispersal of moose from high density areas to low density areas (Cederlund *et al.* 1987, Sweanor and Sandegren 1989) or by reduced calf recruitment (Sweanor and Sandegren in press). Heavy browsing pressure, high population densities and incidences of intraspecific aggression did not result in dispersal. Even in areas with high moose densities where pine plantations were browse damaged, moose were traditional in their range utilization. In Furudal, cows with different patterns of winter and/or summer range use had different rates of calf recruitment. Surprizingly cows with the highest calf recruitment had a movement pattern that included over-wintering in an area of extreme pine damage (by timber industry standards). Damage levels causing reduction in the values of timber should not be expected to lead to natural reductions in the numbers of moose.

The distribution and abundance of moose in Sweden are greatly affected by their movements. Migration allows moose to occur in greater abundance because migratory moose are able to exploit resources that might otherwise remain unavailable and unused. During summer, moose may utilize feeding areas that are inhospitable in winter then migrate up to 100 km, as did some moose in this study, to winter habitat. Seasonal return migration had extreme effects on the seasonal dynamics of moose distributions and local densities in Furudal. No-return dispersal, because of its limited occurrence, had much less effect on total distribution but may still be important for introducing genetic variation.

Differential survival and reproduction of moose with different movement patterns can be one mode of long-term distribution change in this population. During these studies the migratory behavior of moose was predictable in response and was self-replicating. Moose distributions should change as long as there was differential survival and reproduction of moose with different movement patterns. The traditional behavior of seasonal migration and the variable recruitment of cows with different movement patterns may function as both a seasonal and long-term mode of redistributing the population in response to environmental variation. Understanding how these changes in moose abundance and distribution occur has been an essential component in the development of effective moose management in Sweden.

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