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HABITAT DETERIORATION AND THE MIGRATORY BEHAVIOUR OF MOOSE (*ALCES ALCES* L.) IN NORWAY

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SUMMARY

(1) The population of moose (*Alces alces*) at Gausdal Vestfjell in central Norway migrate from low-lying summer areas to winter areas situated at higher altitudes. This is contrary to the general pattern of migration among herbivores.

(2) Archaeological evidence along the migration route shows that the migratory behaviour of this population follows a traditional pattern that has been unchanged since 5000 B.P. despite a deterioration in the quality of their winter range through the loss of high quality pine forests.

(3) The low calf production of the GV population (0.6 calves per cow ≥ 2 years), compared with neighbouring populations (0.79–1.27 calves per cow ≥ 2 years) are likely to reflect poor winter ranges.

(4) Migratory traditions in moose appear to lag behind environmental changes, and changing migratory routes to utilise better quality range may take many generations.

INTRODUCTION

The reproductive performance of moose (*Alces alces* L.) is related to differences in body weight, which in turn is related to variation in range conditions (Sæther 1985), as in other cervid species (e.g. Clutton-Brock, Guinness & Albon 1982; Langvatn & Albon 1986). Consequently, herbivores should adopt feeding strategies that maximize the intake of digestible energy and essential nutrients (Westoby 1978; Belovsky 1984). Because food quality and quantity are not distributed evenly, behavioural patterns that effect the selection of seasonal home range are likely to influence fitness. Not surprisingly, the spring migration of northern temperate herbivores coincides with the 'green-up' (e.g. Le Resche 1974; Adams 1982; Marchinton & Hirth 1984). Moose, for example, normally migrate from low altitude winter areas to higher altitudes during spring (Cederlund, Sandegren & Larsson 1987) because better food quality occurs at higher altitudes (Riley & Skjelvåg 1984).

Migratory moose exhibit philopatry to their winter ranges even at varying population densities, snow conditions and forest damage (Sweaner & Sandegren 1989). However, their data represent a relatively short time frame, and conditions conducive to dispersal (e.g. extreme habitat changes) did not occur during their study. In this paper I present data which show that a herd of Scandinavian moose retains a traditional migration pattern, even though their winter range has deteriorated in quality and their reproductive rate is low.

STUDY AREA

The winter study area was situated in the Gausdal Municipality in Oppland county in Central Norway at 61°N (Fig. 1). It consisted of a 40-km² subalpine winter area, Gausdal Vestfjell (GV), located between 850 and 1000 m, which was dominated by a mixture of

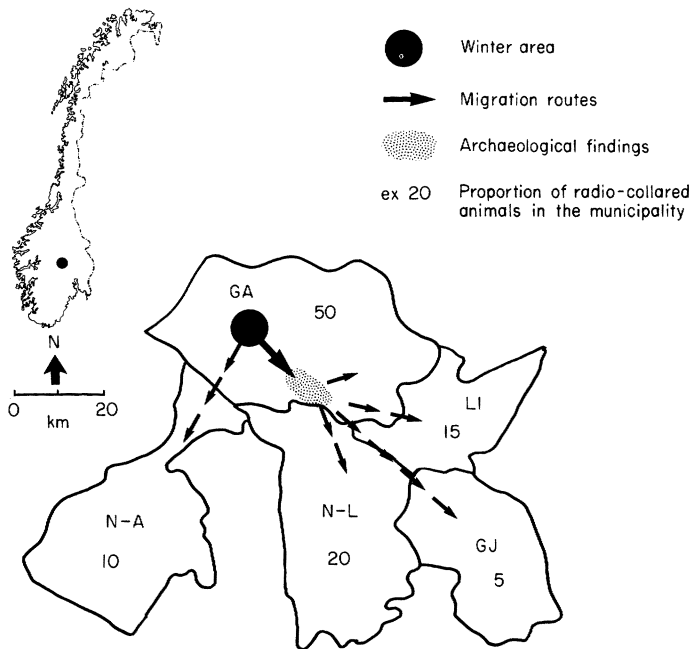


FIG. 1. Moose migration routes from the winter area (■) down to the summer areas. Shaded area represents area with archaeological findings. Numbers within each municipality refer to distribution of radio-collared animals (as percentage of total radio-collared). GA, Gausdal; LI, Lillehammer; GJ, Gjøvik; N-A, Nord Aurdal; N-L, Nordre-Land.

young, heavily browsed, and old forests of brown birch (*Betula pubescens* L.). Deep snow during February–April force the moose to travel in snow exceeding 70 cm in depth (Sæther & Andersen 1990). However, due to the continental climate, the snow is loose with a low density. In contrast to the usual migration pattern, the GV population of moose migrate down to lower areas, lying between 100 and 700 m in summer. The summer area, which contains five municipalities (Fig. 1), is dominated by coniferous forests, interspersed with extensive areas of grey alder (*Alnus incana* L.) and brown birch. White birch (*B. pendula* L.) typical of the agricultural landscape is also common. The GV population constitutes only a fraction of the total moose population in the five municipalities (see Results).

METHODS

Migration behaviour

Aerial censuses with a fixed wing aeroplane were conducted in March during 1980–83 to estimate number of moose on their winter ranges. Although the variable sightability of moose may preclude making accurate population estimates (Gasaway, Dubois & Harbo 1985), the annual use of the same trained staff secured sufficient data. The number of moose migrating to summer ranges situated at lower altitudes were estimated by track counts during April and May in the same period. The census lines intercepted the migration route, and tracks were easily detected in the snow and counted twice a day.

During February 1984–87 a total of fifty moose in GV were immobilized, weighed and equipped with radio-transmitters (142 MHz) (Sæther & Andersen 1990). Eighteen of

these were adult cows, four were adult bulls, two were yearlings and twenty-six were calves. All of the calves were born to radio-collared cows. Moose were radio-located both from the air and the ground during February–August each year.

Habitat changes

Biostratigraphical studies and radiocarbon dating show the winter ranges for moose in GV have changed dramatically from Stone Age to recent times (Hafsten 1985). The forests of Scots pine (*Pinus sylvestris* L.) were succeeded by brown birch (*B. pubescens* L.) interspersed with stands of Norway spruce (*Picea abies* L.), due to a climatic deterioration postulated to have taken place 280 B.P. (Hafsten 1985). Consequently, compared with other winter ranges in Norway, moose in GV are offered browse of low quality. For example, moose in GV were offered twigs with a 5% lower *in vitro* digestibility compared with moose in a northern area in Norway, causing a significantly lower net intake of forage (Sæther & Andersen 1990).

Population parameters

On their summer areas the number of calves born to radio-collared adult cows was checked during June and July. To test whether the GV population had a lower reproductive rate than other moose in the same summer areas, the calf production of adult cows (≥ 2 years) in the five different municipalities used by the GV population, was estimated from hunting observations. In order to use these observations in comparisons with data from radio-collared animals, a stable population density, 50:50 sex ratio of born calves and a constant winter mortality of calves were assumed. Culling data from the five municipalities indicated a relatively stable population density in the period 1985–87, with a 7% S.D. of mean (485.7 ± 33.6) (Central Bureau of Statistics 1987). Winter mortality of moose calves in Norway is generally low. Only 5 of 105 calves born to radio-collared cows in Norway died during the winter (B.-E. Sæther & R. Andersen, unpublished). When estimating the proportion of yearlings in the hunting observations, a 5% winter mortality of calves in the preceding year was assumed. Body weight of calves and proportion of females without a calf are assumed to reflect range conditions (Sæther & Haagenrud 1983), and these parameters from the GV population were compared with data from radio-collared moose in two other areas, one in southern (Aasnes) and one in northern Norway (Troms), using analysis of variance.

RESULTS

Stability of migration pattern

Track counts and radio-location of migrating moose revealed that 65–79% of the animals on the winter ranges in GV, migrated down to lower summer areas (Table 1). Locations of radio-collared moose in 1984–87 showed that a mean of nineteen out of twenty-four moose migrate each year, and no variation in migratory vs. statutory behaviour was found. All of the eighteen different cows occupied the same summer and winter areas in successive years. In addition, only two of a total of fifteen yearlings radio-located during summer, established summer ranges separate from their dams. Both these yearlings were driven off by their mothers before they reached the calving ground, probably due to imminent calving.

The summer area of the moose which migrated from GV covered five different municipalities (Fig. 1). Assuming that the fifty different radio-collared animals were

TABLE 1. Mean number of moose on winter areas in Gausdal Vestfjell (GV) and mean number of migratory moose in 1980–83 and in 1984–1987

Years	Mean number of moose	Range	Mean number of migrating moose	Range	Mean percentage migrating
1980–83*	263	216–319	166	127–203	63
1984–87†	24	20–26	19	16–21	79

* Based on aerial census and track counts.

† Based on radio-collared moose.

representative of the winter population in GV, half the migratory moose spend the summer in Gausdal municipality but at lower altitudes than in GV. The other half move to summer areas in four neighbouring municipalities (Fig. 1). If we expect a 30% culling of the total moose population in the five municipalities, the estimated summer population will be >1600 moose. The migrating GV population numbering approximately 250 animals therefore constitutes only a fraction of the total moose population and is hereafter termed a deme.

Fitness-related parameters for the deme

Estimations based on hunting observations, showed that the number of calves born to adult cows (≥ 2 years) varied from 0.79 to 1.27 in five different municipalities during 1985–87 (Table 2). The lowest calf–cow ratios were found in Gausdal municipality, which had the highest proportion of the migrating deme (24.7%, Table 2), whereas the highest production was found in Gjøvik municipality which had the lowest proportion of the

TABLE 2. Number of calves born per adult cow (≥ 2 years) estimated mean moose population in the period 1985–87 in Lillehammer (LI), Gjøvik (GJ), Gausdal (GA) Nordre-Land (NL) and Nord-Aurdal (NA) municipalities. Calf production of migratory radio-collared cows from GV in the same areas is also included. n =no. of cows

Area	No of calves per adult cow			Estimated‡ mean moose population	Estimated proportion of GV population in summer ranges (%)
	\bar{x}	S.E.	n		
LI*	1.16	0.21	216	178 \pm 17	21.0
GJ*	1.27	0.13	478	428 \pm 84	2.9
GA*	0.79	0.10	598	507 \pm 29	24.7
NL*	1.20	0.07	226	258 \pm 155	19.4
NA*	1.04	0.23	336	249 \pm 32	10.0
GV†	0.60	0.06	18		

* Based on hunting observations.

† Based on radio-collared cows.

‡ Based on 30% culling of total population.

TABLE 3. Live weight of calves in February, and proportion of adult females (> 2 years) without calf in the migrating moose deme in Gausdal Vestfjell (GV) compared with a southern (Aasnes) and a northern (Troms) population. All data based on radio-collared animals

Area	Winter live weight of calves (kg)			Proportion of adult female (> 2 years) without calf	<i>n</i>
	<i>x</i>	S.D.	<i>n</i>		
GV	129.1	18.5	9	0.36	22
Aasnes	146.1	9.3	14	0.00	23
Troms	151.8	29.7	16	0.09	52

migrating deme (2.9%, Table 2). The calf production of radio-collared cows (≥ 2 years) in the migrating deme averaged 0.6 in the same period (Table 2). This low production was due to high age at maturity (R. Andersen, unpublished), a low twinning rate, and infrequent consecutive-year calf production by older cows. In the GV population 36% of adult cows had no calves during 1985–87, compared with 0% and 9% for radio-collared cows in two other populations (Table 3).

Live winter weights of calves born to cows from winter ranges other than GV were not available. However, comparisons of live weights with two other geographically separated populations showed that calves born to cows from the migrating deme were 12–15% lighter in February than calves born to radio-collared moose cows in two other areas ($F = 3.48$, d.f. 2.36 $P < 0.05$, Table 3).

DISCUSSION

In Moose, calves accompany their mother for at least one migration circuit, like most species with long-distance seasonal return migration (Baker 1978). This study and recent investigations in Scandinavia and Alaska (e.g. Cederlund, Sandegren & Larsson 1987; Sweanor & Sandegren 1989; Gasaway, Dubois & Brink 1980) contradict the conclusion that moose have a high tendency to disperse (Waser & Jones 1983). Only calves that were experimentally separated from their dams (Sweanor & Sandegren 1989), and calves of migratory cows that were orphaned in the autumn hunt (Markgren 1975), established winter ranges separate from those of their dams. Therefore, the cow–calf bond, which is maintained through the first autumn migration (Cederlund, Sandegren & Larsson 1987), determines the migratory behaviour and future location of winter range of the calves (Sweanor & Sandegren 1988).

Archaeological findings along the main migration route of the GV population provide evidence of extensive utilization of the migration route by moose from the Stone Age to recent times (Coulson *et al.* 1989). A total of sixty-seven hunting sites and three rock carvings of moose from 5000 B.P. to the bronze age and the location of 124 moose pit-fall traps used in the period 400 B.P. to A.D. 1600, have been found to intercept the main migration route (Coulson *et al.* 1989). Thus, the migratory behaviour of the GV deme has been unchanged for several thousand years, despite dramatic changes in winter range quality (Hafsten 1985).

Although ruminants have evolved simultaneously with their food supply (Moir 1968; Van Dyne *et al.* 1980), they have not overcome the limitation on food intake imposed by high crude fibre requirements (Van Soest 1983; White 1983). On their winter areas the

migrating GV deme have access only to birch of low quality. Compared with a northern moose population, twig digestibility in GV was 5% lower (43.5% vs. 38.5% *in-vitro* digestibility, in the northern area and GV, respectively (Sæther & Andersen 1990). These differences strongly affect the time–energy budget of the animals. Compared with the northern moose population, moose in GV had 13 min longer ruminating periods and 19.5 min shorter foraging periods, which in turn affect the net energetic gain (Sæther & Andersen 1990).

I suggest that low calf production of the GV deme reflects poor range conditions during winter. Twinning rates can be used to assess the quality of moose ranges (Franzmann & Schwartz 1985) and, in general, low reproductive rates are associated with poor range conditions and/or severe winter climate with deep snow and low temperatures (Markgren 1974). Fecundity rates of moose are correlated both with age and carcass weight (Sæther & Haagenrud 1983), and the level of nutrition experienced by a calf during its first winter determines whether puberty is attained the following autumn (Pimlott 1959). Although comparisons could only be made with geographically separated populations, the low winter live weights of calves born to cows in the GV deme, suggests that poor range conditions in GV explain the low reproductive rate for this migratory deme.

Although many biologists have documented that habitat type and resource availability can affect the development of a specific behavioural strategy (e.g. Barash 1974; Sussman 1977; Berger 1979; Armitage 1981; Fox, Rose & Meyers 1981; Stamps 1983), this study demonstrates that the evolution of a tradition can lag behind environmental change, and that behavioural adaptation in ranging patterns to maximize the intake rate may take many generations to evolve (Clutton-Brock & Harvey 1979; Albon & Langvatn, *in press.*).

It appears that moose do not exhibit opportunistic philopatry (see Waser & Jones 1983), nor do they disperse when habitat deterioration warrants it. Hence, the potential for moose populations to be philopatric should not be underestimated (Sweaner & Sandegren 1989).

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