DISPERSAL AND MIGRATION IN NORTHERN FOREST DEER — ARE THERE UNIFYING CONCEPTS?

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ABSTRACT: I summarize studies of natal dispersal and seasonal migrations in 5 species of forest deer: moose (*Alces alces*), roe deer (*Capreolus capreolus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and black-tailed deer (*O. h. columbianus*). Six main features of behavior characterize dispersal in these species: season of dispersal; biased or equal dispersal by the sexes; dispersal in relation to animal density; dispersal in the presence of adult aggression; pre-dispersal excursions; and dispersal distance. These traits are highly variable among and within species and also vary in their proximate causation: mate and resource competition; avoidance of inbreeding, and founder effect. Seasonal migrations are common to all 5 species. These movements are the result of many generations of summer dispersal, and a return to a traditional winter range. Although dispersal appears flexible in relation to different environmental conditions, seasonal migration is a more rigid system of behavior across species. Snow is a key triggering factor and determines occurrence and extent of migration. Snow depth and weather, not plant phenology, appear to determine onset of migration in spring and autumn. Also, the strong tradition in use of seasonal ranges are shared by the species. Summer range located at higher elevation than the winter range is typical of northern cervids in alpine landscapes. Nevertheless, more research is needed to understand relationships among altitude, range quality, and migration patterns of northern deer.

Dispersal was defined by Howard (1960: 159) as: "the permanent movement an individual makes from its birth site to the place where it reproduces or would have reproduced had it survived and found a mate." He also added as an additional requirement that home ranges of young should not overlap those of their mothers. Dispersal generally takes place during summer and may bring animals into regions not favorable for winter survival (Sinclair 1984). Migration presumably evolved as a learned return movement to the natal (first year) winter range (Sinclair 1984, McCullough 1985). In line with this model, dispersal and migration are closely interrelated and determine the large-scale use of the landscape by animal populations.

During recent decades, movements of northern ungulates have been extensively studied with radio-telemetry. Little research, however, has been conducted across species and a comparison and synthesis of the knowledge acquired has not been compiled. This review summarizes studies of natal dispersal and seasonal migration in browsers (Hofmann 1989) among northern deer: moose (*Alces alces*), roe deer (*Capreolus capreolus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and black-tailed deer (*O. h. columbianus*). Hereafter these 5 species are referred to as "forest deer".

Dispersal and migration in forest deer

are important from a management viewpoint. Migration often implies movement between seasonal habitats of critical importance to species, but also may result in large concentrations of animals on winter range. Dispersal relates to the replacement of harvested animals, to range expansion, to the survival and sound management of small isolated populations, and to the concept of habitat sources and sinks. All 5 species of deer have evolved via selection from forces of northern boreal forests, and common features in their dispersal and migration should be expected. Understanding these movements in 1 species, therefore, may help our understanding of similar behavior in the other species.

Deer Dispersal — Proximate Hypotheses and Main Characteristics

In their extensive and classic reviews, Greenwood (1980) and Dobson (1982) noted that patterns of dispersal differ in relation to mating systems. In general, both sexes disperse in monogamous species, whereas in polygynous and promiscuous species, predominantly males disperse. Greenwood (1980) and Dobson (1982) suggested that although females are philopatric because of the advantage of securing resources in a familiar area, males, because of strong competition for females among polygynous and promiscuous species, tradeoff foraging efficiency for greater mating success by dispersing. In monogamous species, mate competition is of less importance, and sex-biased dispersal should not be expected; rather, dispersal should result from competition for resources.

Avoidance of inbreeding is another factor suggested to cause sex-biased dispersal. Pusey (1987) and Wolff (1994) noted that in most mammalian societies, because of a quicker turnover rate of males than females, mothers are more apt to be present when their sons reach reproductive age,

than are fathers when their daughters attain sexual maturity. Consequently, sons disperse so as not to risk mating with their mothers, and daughters are philopatric (Pusey 1987, Wolff 1994).

Here, I compare these proximate hypotheses for dispersal in relation to 6 behavioral traits, which have been recorded in relation to dispersal in forest deer: season of dispersal; dispersal as a result of adult aggression; pre-dispersal excursions; dispersal in relation to animal density; sex-biased dispersal; and dispersal distance.

Season of Dispersal

In Cervidae the mother-young association is broken prior to the birth of the neonate in spring. Dispersal usually occurs during the second summer of life, however, some animals postpone dispersal until the third summer. Moose disperse during their second summer, usually in June (Cederlund et al. 1987, Labonté et al. 1998), but some individuals also may disperse in autumn at the onset of rut (Cederlund and Sand 1992). In Norway, yearling roe deer generally leave their natal range in late May or early June (Bjar et al. 1991, Linnell et al. 1996). Most dispersal of yearling white-tailed deer takes place during rut in autumn (Hawkins et al. 1971, Kammermeyer and Marchinton 1976, Nelson and Mech 1984), but in a dense population on a refuge in the mid-western USA, dispersal was mainly in spring (Nixon et al. 1991). Within this refuge, there was intense competition for inclusion within existing social groups, while densities were much reduced in surrounding habitats because of hunting (Nixon et al. 1991).

There are no reports of dispersal by northern cervids during winter, and this observation may relate to the probability of survival when traveling. In white-tailed deer, dispersal and formation of new home ranges by subadults extended over 2 - 3 years (Nelson and Mech 1984). In moose,

distance between adult females and male young (measured as distance between centers of home ranges) increased steadily up to 3-4 km by the 4th year of life, whereas female young maintained a distance of approximately 1 km from the adult female, beginning in the second summer (Cederlund and Sand 1992).

Dispersal as a Result of Parent and Adult Aggression

Wolff (1993) suggested that except in special instances, forcing offspring to disperse into hostile territories or social groups usually is not an adaptive strategy for parents. Nevertheless, Chesser and Ryman (1986) noted that dispersal is selected for when competition is reduced between close relatives. The total genetic transfer by the individual to the next generation may be increased if dispersal allows more matings by relatives than if emigrants had stayed at home (i.e., increased inclusive fitness).

In roe deer, the only northern forest deer that defends a territory, yearlings with heavier body mass and large antlers disperse at an earlier age than smaller individuals (Strandgaard 1972, Ellenberg 1978). Wahlstrøm (1994) concluded that this outcome was caused by male-male aggression, because antagonism towards yearlings increased during the rut and was mainly directed toward the most sexually mature individuals. Competition for mates, therefore, was the most likely ultimate cause behind adult (i.e., father) aggression in roe deer. If competition for food was the primary reason for adult aggression, as has been suggested by Bobek (1977), dominant males should evict all juveniles regardless of their degree of sexual maturity (Wahlstrøm 1994). Natal dispersal following aggression by adults has been suspected in several studies of forest deer (Hawkins and Klimstra 1970, Kammermeyer and Marchinton 1976, Nixon et al. 1991), but

conclusive evidence was provided only by Wahlstrøm (1994).

Pre-dispersal Excursions and Animal Density

In both roe deer and white-tailed deer, juveniles perform excursions just prior to final dispersal from their natal ranges (Garrot et al. 1987, Bjar et al. 1991, Nixon et al. 1991, Nelson and Mech 1992, Wahlstrøm and Liberg 1995a, Nelson 1998). Excursions may be up to several kilometers from natal home ranges and last from 1-2 days to 2 weeks. When young finally move away from high-density areas, they usually choose a route that minimizes encounters with resident animals (Strandgaard 1972, Nixon et al. 1991, Wahlstrøm and Liberg 1995a). Wahlstrøm and Liberg (1995a) suggested that such excursions aided individuals in estimating population density and the appropriate dispersal route. If this behavior occurs, dispersing juveniles generally should avoid areas of high density, and disperse into low-density areas. That outcome has been observed in several studies of roe deer, moose, and white-tailed deer (Kammermeyer and Marchington 1976, Ballard et al. 1991, Nixon et al. 1991, Sæther and Heim 1993), but exceptions also exist where dispersing animals show no tendency to select high-density areas (Wahlstrøm and Liberg 1995a), even though movements were highly directional (Kilgo et al. 1996). Gasaway et al. (1989) reported no evidence of increased use of abundant browse in recently burned areas by dispersing yearling moose in Alaska, USA. That finding was in contrast to high rates of immigration into a burned area observed by Peek (1974) in northeastern Minnesota. The difference observed in these 2 studies may be accounted for by much higher prefire densities of moose in Minnesota (0.9/km²) than in Alaska (0.1/km²), combined with abundant forage outside the burned area in Alaska

(Hundertmark 1998).

Dispersing animals may react to population density in relation to food resources either according to "ideal free" or "ideal despotic" distributions (Fretwell and Lucas 1970). In an ideal free distribution, animals are free to move between habitats and, thus, tend to assort themselves according to resource availability and the rules of optimal foraging theory (Pyke 1984), resulting in fitness being equal over a spectrum of habitat qualities. Wahlstrøm and Kjellander (1995) reported that fitness parameters (reproduction and body condition) did not vary among females in a local population of roe deer despite considerable difference in population density and habitat quality. They concluded that animals were distributed in relation to resources and that female dispersal was "voluntary" and not forced by adult aggression. In moose, however, fitness parameters vary within the same general region (Hjeljord and Histøl 1999, Keech et al. 2000). Sæther and Heim (1993) speculated that, in moose, dispersing female yearlings were forced out of optimal habitats. That observation would fit the ideal despotic distribution (Fretwell and Lucas 1970).

Pre-saturation Dispersal

Pre-saturation dispersal, defined as dispersal being high at low population density and decreasing at high density, has been documented in various species of animals (Borgstrøm 1992, Stenseth and Lidicker 1992, Allen and Sargeant 1993). Wolff (1992) speculated that lack of juvenile dispersal at high population density is because of a "fence effect" of aggressive, territorial males, and ultimately that at high density all habitats are occupied and there is little to gain from dispersing into other areas.

In cervids, pre-saturation dispersal has been documented for both sexes of roe deer. In southern Sweden, 75% of year-lings left their natal range at intermediate population densities, whereas dispersal rate was much reduced both at high and low density (Wahlstrøm and Liberg 1995a). Dispersal in relation to animal density has received little attention in other species of forest deer. For white-tailed deer in the mid-western USA, a slight decrease in dispersal was noted at high density (Nixon et al. 1991). Conversely, an expanding, low-density population of moose in interior Alaska was philopatric (Gasaway et al. 1980).

Wahlstrøm and Liberg (1995a) reported that only male and female roe deer >15 kg in body mass dispersed when dispersal was at a peak; a decline in dispersal at high population density paralleled a decrease in body mass of juveniles. That outcome indicates that only animals of sufficient size and strength could afford to disperse. Survival cost of dispersal was demonstrated in an experiment with white-tailed deer by Holzenbein and Marchinton (1992a); they reported a significantly higher death rate among 8 dispersing, compared with 24, philopatric yearling males. Because both sexes disperse and risk of inbreeding does not varying with population density, presaturation dispersal in roe deer most likely is caused by mate competition in males and resource competition in females.

Sex-biased Dispersal

In studies on white-tailed deer, proportion of males dispersing varied between 59 and 86% compared with 0 and 29% for females (Nelson and Mech 1984, 1987; Dusek et al. 1989; Nelson 1993; Kilgo et al. 1996). Similarly, a study on black-tailed deer showed a higher proportion of males than females dispersing (62 vs. 38%; Bunnell and Harestad 1983). In moose and roe deer, there is no consistent difference in dispersal between the sexes (Gasaway et al. 1980, Cederlund et al. 1987, Cederlund

and Sand 1992, Sæther et al. 1992, Wahlstrøm and Liberg 1995a, Labonté et al. 1998).

Experimental studies on white-tailed deer have added substantially to our understanding of male-biased dispersal (Ozoga and Verme 1985, Holzenbein and Marchinton 1992b): young males did not disperse when their mother was removed. When all adult males were removed in another experiment, yearling males continued to disperse, although there was no sexual competition from older males. The latter experiment was conducted in a large enclosure with supplementary fed animals. Parent removal in rodents has produced similar patterns of dispersal among offspring (Wolff 1992). Those experiments rule out mate and resource competition as the main cause for dispersal in those species. Rather, a safeguard against inbreeding seems to be the most likely cause. This conclusion fits the observation that adult female white-tailed deer dominate and avoid mating with their close kin, such as yearling males, but usually respond submissively to unrelated yearling males (Hawkins and Klimstra 1970). The proximate cause for dispersal among male yearlings, therefore, likely is behavioral domination by older female relatives (Ozoga and Verme 1985, Holzenbein and Marchington 1992a), which usually occurs either during parturition or rut.

Because sex-biased dispersal is so prevalent in white-tailed deer, why does it not occur in roe deer and moose? For moose, some studies show dispersal distances to be so small that both sexes may most appropriately be called philopatric and non-dispersing (Gasaway et al. 1980, Cederlund et al. 1987, Cederlund and Sand 1992). Males often rut within their mothers' home range. Nonetheless, the probability of mating between mother and son or between siblings is probably low because home ranges are large and many other moose share the same range. Also, many years occur before males attain the body mass and antler size necessary to mate (Van Ballenberghe and Miquelle 1993, Stewart et al. 2000).

In roe deer, male dispersal is clearly the result of aggression from adult males. At high density, neither sex disperse and conditions for inbreeding may therefore be present. Nonetheless, recent studies of a high-density, nondispersing population of roe deer on an island in mid-Norway have documented that females may go outside the territory of the local male to mate (Liberg et al. 1998). A possible reason for this behavior is that, by doing so, females will avoid mating with male relatives.

Exceptions to male-biased dispersal observed in white-tailed deer occur in regions with high population densities. In habitat-limited landscapes of the midwestern USA, females disperse to the same extent as do males. That observation is explained by high density of deer and scarcity of forest patches in this agricultural landscape: resource competition is present for both sexes (Sparrow and Springer 1970, Nixon et al. 1991).

Distance of Dispersal

Distribution of dispersal distances in forest deer generally follows a common pattern: most are short (<15 km), but a few may be very long (>50 km). With a given probability of stopping, a theoretical model of dispersal distances may resemble a simple geometric distribution (Buechner 1987), and a good fit to this model has been demonstrated for moose (Labonté et al. 1998).

In 2 studies of moose in Sweden, average distance between adult female and offspring during the first and second summer after separation varied between 1 and 4 km (distance between centers of home ranges; Cederlund et al. 1987, Cederlund and Sand 1992). Corresponding distance was 3.1 km

in Alaska (Gasaway et al. 1980). In Québec, Canada, yearlings dispersed on average 15.2 km from the capture site with no difference between the sexes; moreover, contribution of moose from lightly harvested reserves to moose killed in adjacent heavily harvested areas was generally limited to 5 km from reserves (Labonté et al. 1998). Dispersal distance of roe deer in 2 areas in southern Sweden averaged as little as 2 km (Wahlstrøm and Liberg 1995b). In white tailed deer, average distances of dispersal varied between 6.4 and 19.5 km (Nelson and Mech 1984, 1987; Dusek et al. 1989; Nelson 1993; Kilgo et al. 1996).

In some studies, much longer distances of average dispersal have been recorded. Roe deer at the northern limit of their range in Sweden dispersed an average of 120 km (Wahlstrøm and Liberg 1995b), and in mid-Norway, in interior valleys with heavy snow, an average 51 km (Linnell et al. 1996). Moose in northern Norway dispersed at least 20-30 km and some dispersed 150-200 km within 1-2 weeks (Sæther and Heim 1993); white tailed deer from a high-density reserve in the midwestern USA, surrounded by fields and scattered patches of forest, dispersed an average of 50 km (Nixon et al. 1991).

The rapid expansion of northern forest deer into a new region also requires longer distances of dispersal than has been recorded in some settled populations. Average expansion rates for 7 moose populations colonizing new areas in North America were 12 km per year (Gasaway et al. 1985). This range expansion occurred even at low population density (Hundertmark 1998) and could be regarded as a type of pre-saturation dispersal.

One reason for long dispersal distances in some areas may simply be that dispersers have to travel farther to reach suitable habitats (Linnell et al. 1998). Nonetheless, this does not explain why in roe deer at the northern edge of their range, almost all subadults leave their natal sites (Wahlstrøm and Liberg 1995b). Wahlstrøm and Liberg (1995b) speculated that there could be 2 genotypically distinct morphs of animals, "dispersive" and "stationary", and that the dispersive type dominated along the expansion front because stationary animals had not had time to colonize that region. Conversely, this hypothesis does not explain why in some southern populations of forest deer, such as roe deer in southern Norway, and white-tailed deer in the midwestern USA, dispersal usually involves long-distance movements. Also, archaeological evidence such as hunting pits, showed that far-dispersing moose in northern Norway had been present in that region for thousands of years (Hohle 1960).

In general, dispersal distance is expected to relate to the balance between the benefits and costs of staying versus moving. Although long-range dispersers risk both increased mortality and not finding a mate, there is also a benefit to be gained: through the founder effect, the genotype of individuals that successfully colonize a new area may dominate the gene pool of a large region.

I expect the relationship between short- and long-distance dispersal in forest deer to have consequences on the spatial distribution of genotypes. Recent studies show significant genetic heterogeneity over short geographic distances in both moose (Ryman et al. 1980, Chesser et al. 1982) and white-tailed deer (Cronin et al. 1991). That result indicates the existence of subpopulations with short dispersal distances and limited exchange of alleles. The relationship between population genetics and dispersal has not been thoroughly examined, but may add substantially to our knowledge of both breeding structure and current and historical gene flow.

Alces

Unifying Concepts?

Dispersal is a highly flexible response to varying environmental conditions (Table 1). Although the hypothesis of mate or resource competition, avoidance of inbreeding, and founder effect, all may explain dispersal in northern forest deer, the importance of each potential cause varies between and within species, depending upon environmental factors. Although moose, roe deer, white-tailed deer, black-tailed deer, and mule deer are all polygynous species, they differ in degree of sex-biased dispersal. There is an almost uniform occurrence of male-biased dispersal in *Odocoileus*, but this behavior is lacking in moose and roe deer. In roe deer, territorial adult males evict younger males, whereas among *Odocoileus*, hostility appears to be from adult females. Differences in range use, territoriality, and possibly cohesion of related maternal groups all may play a role in such differences. Resource competition and animal density appear to be other important causes of variance in sex-biased dispersal. The only study where sex-biased dispersal was absent in white-tailed deer was in the fragmented, high-density habitats of the midwestern USA. In moose, as the other forest deer, the founder effect is likely to play a role when animals expand into new ranges (Table 1). Virtually all dispersal studied in moose, however, involves animals moving into areas already occupied by others and this dispersal is poorly understood.

Table 1. Summary of pre-dispersal and dispersal characteristics of moose (*Alces alces*), roe deer (*Capreolus capreolus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and black-tailed deer (*O. h. columbianus*), and alternative proximate hypotheses to explain them (parentheses indicate a "suspected cause").

|	Proximate Hypothesis			
Characteristics	Competition for resources	Competition for mates	Avoidance of inbreeding	Founder effect
Adult aggression		*C. capreolus*[1]		
Pre-saturation dispersal	*C. capreolus* females[2]	*C. capreolus* males[2]		
Sex-biased dispersal			*Odocoileus* spp.[3]	
Long distance dispersal	(*Odocoileus* spp.)[4]			(*A. alces*[5], *C. capreolus*[6], *Odocoileus* spp.[4])
Pre-dispersal excursions	(*C. capreolus* females[7,8], *Odocoileus* spp.[4,9,10])	(*C. capreolus* males[7,8], *Odocoileus* spp.[4,9,10])		

[1]Wahlstrøm 1994. [2]Wahlstrøm and Liberg 1995a. [3]Nelson and Mech 1984, 1987; Dusek et al. 1989; Nelson 1993; Kilgo et al. 1996; Bunnell and Harestad 1983. [4]Nixon et al. 1991. [5]Sæther and Heim 1993. [6]Linell et al. 1996. [7]Bjar et al. 1991. [8]Wahlstrøm and Liberg 1995a. [9]Garrot et al. 1987. [10]Nelson and Mech 1992.

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Migration - Outcome of Dispersal and Tradition

Natal dispersal is the only behavioral trait that may distribute large numbers of animals over summer range, and there is evidence that the first summer range occupied by young forest deer becomes their life-long range (Gruell and Papez 1963, Nelson and Mech 1984, Brown 1992, Nelson 1998). From summer range, animals generally return to winter range they used with their mother during the first winter, and this behavior is transferred from mother to young through generations (Nelson and Mech 1981, Tierson et al. 1985, Sweanor and Sandegren 1988). Distances of seasonal migrations, therefore, are the accumulated result of many generations of natal dispersal, and a return to the original winter range. Migrations are, in general, highly directional (Gruell and Papez 1963, Verme 1973, Hoskinson and Mech 1976, Broadfoot et al. 1996, Kilgo et al. 1996, Nicholson et al. 1997, Van Deelen et al. 1998) (Fig. 1); direction and distance of migration often are maintained even in translocated animals (Nelson 1994, Danilkin 1996). Furthermore, this bias in migration direction often is shown in the absence of any apparent physical barriers to movement (Verme 1973, Broadfoot et al. 1996, Kilgo et al. 1996, O. Hjeljord, unpublished data) and may have evolved when parts of the ranges were initially colonized, and animals dispersed into remaining low-density areas. Indeed, seasonal migrations retrace the expansion of animals into a new area (Pulliainen 1974). Major winter ranges are habitats that offer good conditions year-round; in the boreal forest, those are generally the riparian communities of large river valleys (Mercer and Kitchen 1968, Coady 1980, Telfer 1984). As range expands through summer dispersal, some animals may settle in new year-long ranges and become stationary. Dispersal from those new ranges may produce

Fig. 1. Some main winter ranges of migrating moose in Scandinavia together with directions and distance to summer ranges. Animals moving >10 km between seasonal ranges are considered migratory. Data from the literature on radiocollared animals (Sandegren and Sweanor 1988, Lorentsen et al. 1990, Sæther and Heim 1991, Cederlund and Sand 1992, Sæther et al. 1992, Histøl and Hjeljord 1993, Bjerga 1996, Odden et al. 1996, Gunneng 1997; L. Kastdalen, Høgskolen i Hedemark, Koppang, Norway, unpublished data; F. Sandegren, Swedish Sportsmen's Association, Uppsala, Sweden, unpublished data).
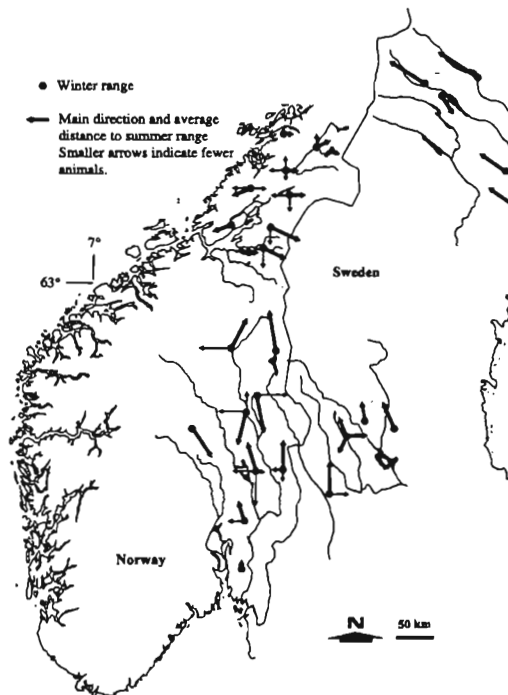
surprising patterns of movement, sometimes migrations in opposite directions to initial ones (McCullough 1985) and overlap between summer ranges of animals belonging to different winteryards (Gruell and Papez 1963, LeResche 1974, Brown 1992, Sæther et al. 1992).

Snow generally is regarded as the factor that restricts forage availability and animal movement over much of summer range of northern forest deer, thereby forcing a migration to more favorable winter ranges.

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Several characteristics of seasonal migrations may be explained solely by this forage-locomotion hypothesis.

Arguments in Favor of the Forage-locomotion Hypothesis

Seasonal migrations are characteristic of areas of large temporal variations in forage conditions. — Generally, the migrating proportion of animals in a population of forest deer increases with the number of days snow stays on the ground (Danilkin 1996). In southern Sweden and continental Europe, roe deer are mostly nonmigratory (Wahlstrøm and Liberg 1995a, Holand et al. 1998), whereas these deer have distinct seasonal migrations in Norway (Bjar et al. 1991, Mysterud 1999). Scandinavian moose are generally nonmigratory in coastal lowlands with little snow, but have extensive migrations farther inland (Fig. 2). White-tailed deer in the northern USA are migratory (Hoskinson and Mech 1976), but are generally nonmigratory year-round in southern states such as Florida, Texas, and Arizona (Inglis et al. 1979).

In areas of varied topography, winter range generally is at lower elevation than summer range. — Areas of lower elevation generally have less snow and, therefore, offer better locomotion and more available forage during winter. Moose (Hauge and Keith 1981, Sweanor 1987, Sæther et al. 1992), roe deer (Mysterud 1999), black-tailed deer (Loft et al. 1984; Schoen and Kirchhoff 1985, 1990), and mule deer (Garrot et al. 1987, Nicholson et al. 1997) generally migrate to low elevations during winter.

Migration to winter range ceases during mild winters with little snow. — Although there is a strong element of tradition in migration of cervids, snow appears to be a key stimulus for its release. When snow arrives late, autumn migration is de-

Fig. 2. Proportions of stationary and migratory moose in different regions of Scandinavia. Animals moving >10 km between seasonal ranges are considered migratory. Data from the literature on radiocollared animals (Sandegren and Sweanor 1988, Lorentsen et al. 1990, Sæther and Heim 1991, Cederlund and Sand 1992, Sæther et al. 1992, Histøl and Hjeljord 1993, Bjerga 1996, Odden et al. 1996, Gunneng 1997; L. Kastdalen, Høgskolen i Hedemark, Koppang, Norway, unpublished data; F. Sandegren, Swedish Sportsmen's Association, Uppsala, Sweden, unpublished data).
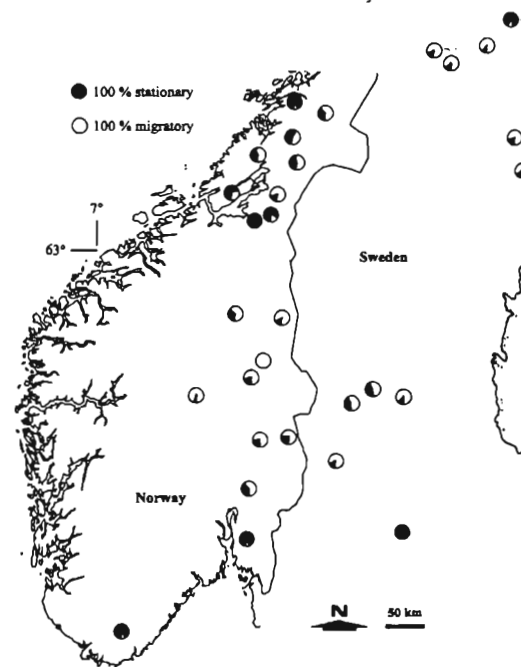
layed in moose (Ballard et al. 1991, Sæther et al. 1992) and white tailed deer (Drolet 1976). With shallow snow, moose (Van Ballenberghe 1977, Sæther et al. 1992), mule deer (Garrot et al. 1987, Brown 1992), and black-tailed deer (Schoen and Kirchoff 1985) may remain on the summer range or move only part way to winter range. If snowfall occurs during spring migration, white-tailed deer frequently return to winter range (Drolet 1976, Tierson et al. 1985).

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Arguments Against the Forage-locomotion Hypothesis

Often deer seem to travel much farther than necessary between available winter and summer ranges. Summer ranges left by some animals may be winter ranges of other animals. — This unexpected distribution is well known for white-tailed deer (Drolet 1976, Hoskinson and Mech 1976, Tierson et al. 1985), mule deer (Gruell and Papez 1963, Brown 1992), roe deer (Holand et al. 1998), and also has been noted in moose (Sæther et al. 1992). The explanation for these sometimes erratic movements between summer and winter ranges must be sought in a strong element of tradition in seasonal migrations. Apparently, when natal dispersal brings an animal to a summer range, which also would be a satisfactory winter range, and that may even be the principal winter range of another subpopulation, the strong element of learning and tradition may, nevertheless, cause long-distance migrations back to the original winter range. One reason for this surprising pattern could be the benefit of being surrounded by the presumably less-aggressive kin (Nelson and Mech 1981, Wahlstrøm and Liberg 1995a).

Onset of seasonal migrations is related to snow depth, temperature, humidity or rut, not to vegetation phenology. — Migration to winter ranges by moose generally is a slow process related to the accumulation of snow and extending for several weeks. Spring migration to summer ranges, conversely, is fast, often taking <1 week (Edwards and Ritcey 1956, Coady 1974, Van Ballenberghe 1977, O. Hjeljord, unpublished data). Moose in mid-Sweden start autumn migrations when snow depth at the summer range is slightly >40 cm (Sandegren et al. 1985). Some early autumn migration may be to avoid traveling in deep snow; in moose inhabiting alpine and northern tundra in North America, autumn migration is to rutting areas located within the winter range and begins in late August prior to the beginning of snow accumulation (Gasaway et al. 1983, Mauer 1998). Roe deer and white-tailed deer generally migrate to winter range well in advance of deep snow (Garrot et al. 1987, Bjar et al. 1991, Mysterud 1999). In white-tailed deer, autumn migration often coincides with a sudden drop in temperature (Verme and Ozoga 1971, Hoskinson and Mech 1976, Nelson 1995) or a combination of low temperature and snowfall (Nelson 1995). In the Cascade Mountains of Oregon, USA, autumn and spring migration of black-tailed deer correlated neither with snow nor temperature, but rather with seasonal changes in minimal relative humidity (McCullough 1964).

In spring, animals apparently do not take advantage of the early growth of forage at low elevation, but move quickly to higher altitude where new growth of plants has not yet been initiated (Edwards and Ritcey 1956, Verme 1973, Hoskinson and Mech 1976, Sandegren et al. 1982, Loft et al. 1984, Sandegren et al. 1985, Mauer 1998). Mysterud (1999) reported that timing of spring migrations was delayed for roe deer with summer home ranges at high altitudes. Verme (1973) and Nelson (1995), however, noted that white-tailed deer left the yard as soon as the weather conditions (mainly snowpack) permitted them to travel freely. Moose leave the lowland just when the first green leaves appear and move towards the high country where they have to wait another 1-2 weeks for new growth to appear (Samdal and Wammer 1996).

This rapid change in use of habitat by cervids is difficult to explain. Several authors noted the importance for females to arrive at the summer range before parturition (Van Ballenberghe 1977, Skogland 1991, Seip 1992). Nonetheless, if rearing and protection of young were the main reasons

for early spring migration of females, I would expect males and barren females to remain in the lowland long enough to take advantage of early plant growth. Sandegren et al. (1985) and Phillips et al. (1973) noted no difference in the onset of migration between male and female moose among 127 and 36 radiocollared animals, respectively.

The proportion of animals migrating as well as the distance of migration may vary between the sexes. — If seasonal migrations evolved from natal dispersal, male-biased dispersal in *Odocoileus* should cause more males than females to migrate between seasonal ranges. Currently, there are too few data to evaluate that assumption. Nevertheless, Nicholson et al. (1997) noted that while all males among radiocollared mule deer were migratory in the Transverse Ranges of coastal California, USA, females exhibited a mixed strategy with both migrant and resident individuals.

In southern Sweden, most female roe deer undertook migrations only as yearlings, whereas males did not migrate (Wahlstrøm and Liberg 1995a). Return of yearling females to their natal range in autumn fits the hypothesis of Nelson and Mech (1981) that protection from predation given by social groups is the main reason for migration, (i.e., it is necessary to migrate to be social). When female roe deer established winter groups with their own young, migration stopped. Yearling males are dominant over females, and it was speculated that the males could enter any female group they liked and, therefore, had no need for migration back to their own kin on the natal range for group protection (Wahlstrøm and Liberg 1995a). Conversely, in southern Norway, both sexes of roe deer migrate, females generally move the longest distances, and there is no indication that migration of females ceases with time (Bjar et al. 1991, Mysterud 1999).

Choices of seasonal ranges do not appear optimal. — Summer range located at higher elevation than the winter range is typical of northern cervids in alpine landscapes. Traditionally, this pattern has been explained by an improvement of the nutritive value of forage with increasing altitude (Bliss 1962, Klein 1965, Albon and Langvatn 1992). Nonetheless, various studies on this relationship are not conclusive. Albon and Langvatn (1992) reported that autumn body mass of red deer (*Cervus elaphus*) with summer ranges at high altitude were higher than for animals with summer ranges at low altitude. Hjeljord and Histøl (1999), however, noted the opposite relationship for moose. Furthermore, roe deer and black-tailed deer had larger summer ranges at high compared with low altitude (Loft et al. 1984, Mysterud 1999). This indicates that these areas are of low quality because the size of home ranges during summer reflects resource levels in these species (Wahlstrøm and Kjellander 1995, Tufto et al. 1996). More studies on the relationship between range quality, altitude, and migration patterns are clearly needed.

Some moose populations have winter range situated at higher elevation than summer range, apparently because of more shallow and loose snow at those high-altitude ranges (Gasaway et al. 1983, Mauer 1998). Furthermore, moose may use several behavioral adaptations to cope with winter conditions in mountainous, treeline habitats (Van Ballenberghe 1992). Nevertheless, an extreme example of a non-optimal pattern of migration occurs in central Norway. Here, moose from the lowlands ascend to winter ranges of deep snow at high altitude, with concomitant decrease in reproduction and fitness (Andersen 1991). Number of young born per adult female is only 0.6 in this population compared with 1.04-1.27 in the surrounding populations wintering at low altitude. That movement

pattern should not be regarded as a tradeoff resulting from a search for winter range against a gradient of deep snow. This wintering ground contains the only area of pine (*Pinus sylvestris*), an important winter forage for moose, in a region totally dominated by spruce (*Picea abies*); this range once may have been a good year-round habitat. With increasing population density, animals dispersed to better ranges during summer. What occurs today is not a migration to a winter range, but a return to an original year-round range. Aboriginal pitfall systems used to kill moose along the migration route indicate that this migration system is very old (Andersen 1991).

Generally, most populations of northern forest deer consist of migrating and nonmigrating individuals. In an evolutionary perspective, there should be a balance so that migrants and nonmigrants have the same lifetime reproductive success (Histøl and Hjeljord 1993, Nicholson et al. 1997). Clearly, strong traditions in movement may be a weak link in this chain.

CONCLUSION
Several characteristics of seasonal migrations are shared by the 5 deer species reviewed here. The most important are rigid and strong traditional use of seasonal ranges together with snow as a key stimulus for migration. The timing of migration, particularly in spring, and its relation to optimal feeding strategy, predator avoidance, and possibly other factors remains, however, poorly understood.

The overriding effect of snow in shaping seasonal migrations in forest deer together with the maintenance of migration direction and distance in dislocated animals (Nelson 1994, Danilkin 1996) are striking. Forest deer display a migration pattern that may approach the definition of migration suggested by Kennedy (1985), who stated that migrants inhibit or suppress inputs from

resources (e.g., passing through good feeding grounds) that otherwise would stop movement, and that migration ceases as a result of physiological changes brought about by the movement itself. In an evolutionary context, this would indicate high survival value of migration in forest deer and, particularly, in returning to a specific and original winter range. Dispersal clearly is more of a conditioned response that has been shaped in a system of counteracting selective factors in which outcome and balance may vary with type of environment and probably also with difference in social organization among species.

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