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Authors: Wahlström, L. Kjell, and Liberg, Olof

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# Contrasting dispersal patterns in two Scandinavian roe deer *Capreolus capreolus* populations

**L. Kjell Wahlström & Olof Liberg**

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Yearling natal dispersal frequencies and distances in roe deer *Capreolus capreolus* were compared between two regions in Scandinavia, Västerbotten, on the northern edge of the expanding population, and Mälardalen, in the central continuous part. Data were collected using telemetry during 1987-1994. In Västerbotten 91% (n = 11) of the males and 100% (n = 9) of the females left their natal areas, and in Mälardalen 43% (n = 42) of the males and 48% (n = 50) of the females dispersed. No intra-regional difference in distances dispersed was found between sexes. Average dispersal distance in Västerbotten was ca 120 km (n = 17), with only one disperser settling less than 39 km from its natal area. In Mälardalen, the average dispersal distance was around 4 km (n = 42), and only two animals moved further away than 15 km. One hypothesis accounting both for the almost complete dispersal of deer in Västerbotten, and for the existence of a few long-distance dispersers in Mälardalen, is that two genotypically distinct morphs of roe deer exist, one 'dispersive' and one 'stationary'. The predominance of the 'dispersive' type in Västerbotten could be explained by 'stationaries' not having had enough time to colonise this region since the last population bottleneck in the mid 19th century, when the Scandinavian population was restricted to the southernmost part of Sweden.

*Key words: Cervidae, dimorphism, dispersal, roe deer, Capreolus capreolus*

*L. Kjell Wahlström & Olof Liberg, Stockholm University, Department of Zoology, S-106 91 Stockholm, Sweden*

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Natal dispersal is an important part of roe deer *Capreolus capreolus* biology, and has been studied over a large part of the species' range in Europe, e.g. in Switzerland (Kurt 1968), Denmark (Strandgaard 1972), France (Bideau et al. 1987, 1993) and in southern Sweden (Wahlström & Liberg 1995). However, these studies have all been carried out in areas where the species has been present long enough for the populations to have reached relatively stable conditions. No dispersal study in recently occupied areas, i.e. on the edge of an expanding population, has been performed to date. There is reason to believe that the dispersal pattern in such areas differs from that in the central continuous part of a population's distribution, e.g. because of free access to attractive neighbouring patches resulting in a higher dispersal rate.

The Scandinavian roe deer population has been steadily expanding its range towards the north since the mid 19th century. In the early 1800s the species occupied the entire southern part of the peninsula, up to approximately 60°N latitude. However, due to abolition of the royal and aristocratic deer hunting monopoly and the introduction of a general permission for peasants to hunt deer, culling pressure increased substantially. Consequently, the population went through a severe bottleneck in the 1830s during which a small relict of less than 100 individuals remained on one estate only in the southernmost part of Sweden (Ekman 1919), where they were protected by the landlord. After reintroduction of strict hunting laws, removal of free-ranging domestic stock, and the successive near extermination of wolf *Canis lupus* and lynx *Felis lynx*, the roe deer population quickly recovered. Within 60 years it reoccupied its former range, and today roe deer occur all over Scandinavia up to approximately 67°N latitude (Fig. 1) leading to a spread of 1,300 km in 150 years with an average speed of 9 km per year. This demonstrates an enormous dispersal capacity, much

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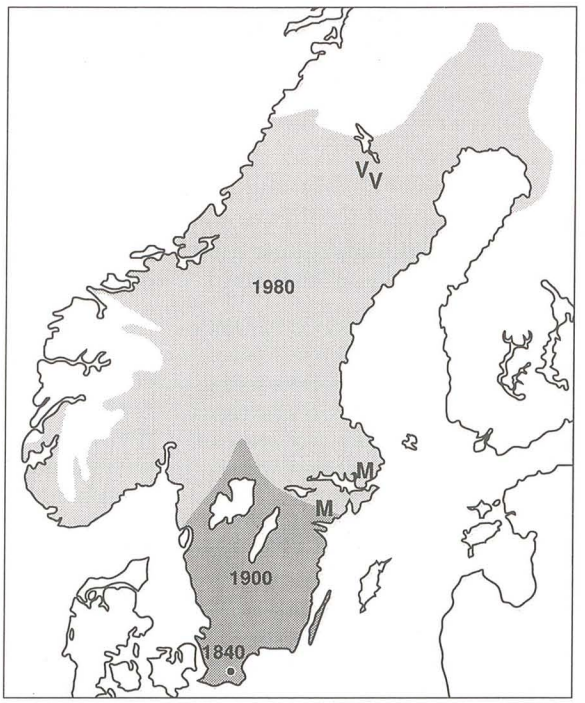


Figure 1. Geographical distribution of the Scandinavian roe deer population by 1840, 1900 and 1980, with indication of the location of the Mälardalen (M) and Västerbotten (V) study sites.

stronger than those reported from the above-mentioned studies in stable populations where dispersal distances amounted to 1-1.5 km per year.

The question we attempt to answer in the present paper is: Does roe deer natal dispersal pattern differ between the edge of an expanding population vs. the central continuous part? We describe natal dispersal frequency and distances travelled before settling on the edge of the expanding population in northern Scandinavia, and compare it with corresponding parameters in the central continuous part in southern Scandinavia.

## Study areas

Two areas in the Västerbotten region in northern Sweden on the edge of the expanding population, and two in the Mälardalen region in southern Sweden in the central continuous part, were chosen as study sites in which predispersal deer were trapped and provided with radio-collars.

The Västerbotten areas, Gunnarn (65°00'N, 17°40'E) and Åskilje (64°54'N, 17°52'E), are located in the northern part of the Scandinavian taiga. This region is almost completely covered by coniferous forest, and only in the river valleys do small and scattered agricultural areas (less than 1% of the total area) around human settlements occur. Forests are commercial and the dominating tree species are Scots pine *Pinus sylvestris* and Norway spruce *Picea abies*, with a small intermix of broadleaved species, mainly birch *Betula spp*. On the farmed fields clover *Trifolium pratense* hay is the dominant crop, besides smaller amounts of cereals like oats *Avena sativa* and barley *Hordeum vulgare*. The climate is characterised by harsh winters and relatively warm and dry summers. January is the coldest month with an average temperature of -12°C and July the warmest with an average temperature of 14°C. Annual precipitation amounts to ca 490 mm with most falling in July and least in March. Snow normally occurs during November-April and average snow depth by 31 January is 120 cm.

Roe deer first became established in this part of Scandinavia during the 1960s. Average deer density is 0-1 deer per km$^2$ with large local differences (Liberg et al. 1995), as the deer population is distributed in more or less isolated 'pockets' around the small agricultural areas in the river valleys. Locally, population density was estimated at 5-10 deer per km$^2$ (Liberg et al., pers. comm.). Density fluctuated little during the study period. About 20% of adults are restricted to the agricultural areas all year round; 45% expand their ranges during the summer to include also the surrounding upland forests, and the remaining 35% migrate between separate summer and winter ranges that rarely are located more than 10 km apart (unpubl. data). Adults thus are faithful to their established home ranges.

Mälardalen is located in the ecotone between the southern taiga and the northern part of the nemoral hardwood zone. The core study sites in this region were Ekenäs (58° 58'N, 16°35'E) and Bogesund (59°24'N, 18°12'E). Both are representative for the entire region with ca $^2/_3$ of the area being covered by commercial forest and the rest by agricultural land. Forests are mainly composed of Scots pine and Norway spruce with a relatively high intermix of broadleaved species like birch, oak *Quercus robur*, aspen *Populus tremula* and alder *Alnus glutinosa*. On the cultivated fields clover hay, rape *Brassica napus* and various cereals such as wheat *Triticum aestivum*, rye *Secale cereale*, oats and barley are grown. The climate is characterised by moderate winters and warm and relatively dry summers. The average temperature in July is 17°C and in February -3°C. Annual precipitation amounts to ca 550 mm, with most falling in August and least in February. Snow normally occurs during December-March with an average snow depth of 20 cm by 31 January.

Roe deer recolonised Mälardalen at the turn of the last century, and average deer density is 10-20 deer per km$^2$ (Liberg et al. 1995). The population is much more homogeneously distributed than in Västerbotten, and with few exceptions adult deer are geographically highly stable. Both study populations in this region underwent marked changes in density during the study period, increasing from 12 to 24 deer per km$^2$ in the Ekenäs area, and from



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12 to 31 deer per km² in the Bogesund area. Furthermore, the former population stabilised, whereas the latter was experimentally reduced to about 7 deer per km² during 1992-1994, as part of an extensive study on roe deer demography (see Liberg et al. 1995).

## Methods

In Mälardalen data were collected during 1987-1994 (Ekenäs) and 1989-1994 (Bogesund); in Västerbotten during 1990-1994. Juveniles were caught either as newborn (at the Ekenäs site only), or at the age of 7-10 month. Newborns were provided with expandable radio-collars (TXT-1Sm; 151 MHz; Televilt International AB, Storå, Sweden) with a life-span of 1.5 years. Older juveniles were captured in box traps during December-March, and aged on the basis of dentition. These animals were provided with radio-collars (TXT-2Sm; 151 MHz) with a life-span of 3.5 years. A Televilt RX-81 and a 4-element Yagi antenna were used for tracking, and radio fixes were obtained by triangulation. Tracking intensity varied from one fix per week to one or more per day during some periods, e.g. during mother-fawn separation. In some of the cases where the radio signals of dispersers were lost, reports on culled marked deer were used to determine dispersal distances. Dispersers in the Västerbotten area were frequently located from aeroplane.

For home range analysis the minimum convex polygon method (Mohr 1947) was applied. A comparison of juveniles caught as newborns with those captured during their first winter (at the age of 7-10 months) showed that ranges obtained for the latter were representative for the natal areas in total.

We defined natal dispersal as the movement to, and occupation of, an area completely non-overlapping with the range frequented during the animal's first year of life together with its mother. Dispersal frequencies were averages over the entire study period. A disperser was considered established in an area after having spent a minimum of three consecutive months within a 'confined' area. This definition of establishment area was based on information from a large number of dispersers that have been followed for several consecutive years. Dispersal distance was defined as the distance between the geometric centres of the natal and establishment area, respectively.

Dispersal frequencies were compared with log-linear models, and ANOVA was used to test for differences in dispersal distances.

## Results

### Dispersal frequencies

On the Gunnarn site a total of eight juveniles (three males and five females) were trapped and provided with radio-collars, all of which left their natal areas as yearlings. Correspondingly 12 juveniles (eight males and four females) were radio-collared in the Åskilje area, of which all but one male dispersed.

In the Bogesund area, where 55 juveniles (28 males and 27 females) were radio marked, 32% of the males and 41% of the females dispersed. On the Ekenäs site, where 37 juveniles (14 males and 23 females) were radio-collared, 64% of the males and 56% of the females left their natal areas.

As we were primarily interested in inter-regional variation, rather than intra-regional variation, data from the two study sites in Mälardalen and Västerbotten, respectively, were pooled. Significance was tested by dropping non-significant terms from the saturated model until all remaining interactions were significant. Only the interaction between dispersal frequency and region was significant ($\chi^2 = 7.3$, df = 1, $P < 0.01$), indicating that the dispersal rate was significantly higher in Västerbotten than in Mälardalen. Dispersal rate did not differ significantly

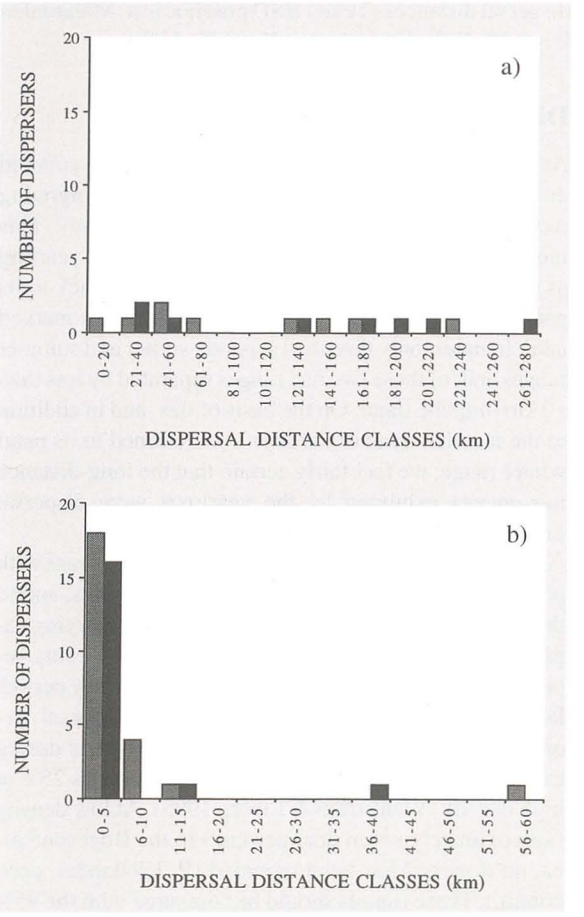



Figure 2. Distribution of female (shaded bars) and male (black bars) dispersal distances (in km) in (a) Västerbotten, during 1990-1994 and (b) Mälardalen during 1987-1994.



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between the sexes ($\chi^2 = 0.19$, df = 1, P = 0.66, N.S.), and the effect of sex did not differ significantly between regions ($\chi^2 = 0.0$, df = 1, N.S.). Consequently, dispersal rate was significantly higher in Västerbotten than in Mälardalen, while dispersal rate was independent of sex.

### Dispersal distances

There was a significant interaction between dispersal distance and area, but not between distance and sex (two-way ANOVA, area effect $F_{(3,50)} = 21.92$; $P < 0.001$; sex effect $F_{(1,50)} = 1.73$, P = 0.19, N.S.; area*sex effect $F_{(3,50)} = 1.49$, P = 0.23, N.S.). Average (±SE) dispersal distance with sexes pooled in the Västerbotten region was 125.1 ± 30.8 km (Gunnarn, n = 7) and 114.9 ± 27.2 km (Åskilje, n = 10; Fig. 2a), and in Mälardalen 2.7 ± 0.5 km (Bogesund, n = 20) and 7.6 ± 3.0 km (Ekenäs, n = 22; Fig. 2b). The interaction between distance and area could thus be ascribed to a difference between regions (Tukey HSD post hoc test, $P < 0.001$ in all inter-regional comparisons), as there were no significant intra-regional differences in dispersal distances (Tukey HSD post hoc test, Mälardalen P = 0.98, N.S.; Västerbotten P = 0.80, N.S.).

## Discussion

As deer in the Västerbotten region were radio-collared during winter only, juveniles of seasonally migrating mothers consequently had unknown birth ranges. This means that there was a small risk of classifying a yearling as a disperser, when it was merely migrating back to its natal summer range. However, among 10 radio-marked adult females, only three had separate winter and summer ranges and, of those two had ranges separated by less than 10 km (unpubl. data). On the basis of this, and in addition to the fact that none of the deer ever returned to its natal winter range, we feel fairly certain that the long-distance movements exhibited by the yearlings were dispersal movements.

Dispersal frequency has been observed to increase with population density up to relatively high densities, and to decrease again as the population approaches carrying capacity (Wahlström & Liberg 1995). While we only reported average dispersal rate over the entire study period, large fluctuations in density, and thus in dispersal frequency, did occur in the Mälardalen study areas during this period. Peak dispersal rate in this region was 75% at high density (Wahlström & Liberg 1995). At low density (approximately seven deer per km$^2$) in the Bogesund area, no dispersal has been recorded (P. Kjellander, pers. comm.). These figures should be compared with the 95% dispersal rate in Västerbotten at a density that can be regarded as low-intermediate (5-10 deer per km$^2$).

One possible explanation for the striking difference in dispersal pattern exhibited by deer in Västerbotten as compared to Mälardalen, may be that it simply is the effect of a difference in the availability of suitable settling sites. High-quality habitat in Västerbotten is rare, and dispersers may inspect the same amount of such habitat both in the south and the north before settling. One result of this is that deer in the north are forced to travel far either before finding attractive patches, or until fatigue forces them to settle in suboptimal areas. In the south, where high-quality habitat is abundant, deer never have to travel far in order to find optimal patches, resulting in the relatively short dispersal distances observed. This hypothesis does, however, not explain the almost complete dispersal of young in Västerbotten, or the existence of a few long-distance dispersers in Mälardalen.

Yet another hypothesis is that deer disperse in order to avoid inbreeding (e.g. Pusey 1987). According to this hypothesis, parent-offspring matings are expected to be highly probable in the relatively small demes of Västerbotten, resulting in almost complete dispersal of young in this region. The long dispersal distances would be explained by the isolation of individual demes. An animal must travel until it encounters another deme in order to secure its reproduction. In Mälardalen unrelated deer frequently live within short distances, allowing subadults to remain philopatric, or to disperse short distances only. Like the first hypothesis, however, this one also fails to explain the existence of long-distance dispersal in the south.

An alternative hypothesis, accounting both for the almost complete dispersal of young in Västerbotten and for long-distance dispersal in Mälardalen, is that two genetically distinct morphs of roe deer exist, one 'dispersive' and one 'stationary'. The 'dispersive' morph should be characterised by a relatively high sensitivity to competitive pressure, e.g. by being less fecund or attaining sexual maturity later than 'stationaries'. Furthermore, it should be characterised by a strong inclination to dispersal and a tendency to travel far, thereby enhancing the possibility of finding a highly attractive patch, i.e. an area with abundant resources and few competitors, before settling. In contrast, the 'stationary' morph should be less sensitive to competitive pressure and therefore characterised by a higher degree of philopatry, or short-distance dispersal only. The 'dispersive' morph is predicted to dominate any population being in the phase of expanding its range. Moreover, populations that have occurred long enough in an area in order for the 'stationary' morph to have been able to colonise it, are predicted to be increasingly dominated by 'stationaries'. However, the persistence of the 'dispersive' type in this situation is to be expected because vacant sites will always arise. Hamilton & May (1977) demonstrated that, even under stable and saturated habitat conditions, there will be selection for



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maintenance of dispersal. The existence of a few 'dispersers' in Mälardalen is in agreement with this line of reasoning.

The phenomenon of polymorphic dispersal behaviour has received most attention from entomologists studying insects exhibiting polymorphism in obvious morphological structures, such as wings, affecting their ability to disperse (for a review see Harrison 1980). Several authors have linked the existence of particular 'dispersive' morphs to the temporal and spatial stability of the environment, with the 'dispersive' morph being increasingly favoured as the persistence of the habitat decreases (see e.g. Denno et al. 1991, McPeek & Holt 1992, Roff 1994).

The idea of a true genetic polymorphism in mammalian behavioural characters has received little attention, which is probably due to the stronger behavioural flexibility of mammals. However, we believe distinct genotypic 'dispersive' and 'stationary' morphs could coexist in a species like roe deer, adapted to exploit ephemeral gaps (burns, windblows, and insect attack) with early succession vegetation in a matrix of mature forest (Cederlund & Liberg 1995, Liberg & Wahlström in prep.). This is an environment characterised by variability both spatially and temporally. According to a recent model by McPeek & Holt (1992), this is the situation where a "...polymorphism of two discrete dispersal types with unconditional dispersal strategies can exist". Also the successive prediction of this model, that "...the phenotypic and genotypic variation for dispersal characters in a species having a dimorphism (rather than continuous polymorphism; our comment) should be small within patches (read Mälardalen and Västerbotten, respectively; our comment) but large between patches", fits our roe deer case well.

A possible scenario for the sequence of events leading to the frequency difference of the two dispersal types that we found between Mälardalen and Västerbotten is as follows: In the small relict population in the southernmost part of Scandinavia 150 years ago both types existed. When the expansion north started, the 'dispersive' morph took the lead in the population spread and was responsible for the extremely rapid recolonisation of the country. The first roe deer reached Mälardalen between 1890 and 1900, i.e. a hundred years ago. For some time the population here consisted entirely of the 'dispersive' type. However, as individuals belonging to our 'stationary' type perform short-distance dispersal (up to approximately 10 km), it is quite possible that they reached Mälardalen in a second wave. Considering that the distance between the original site in southern Scandinavia and Mälardalen is 500 km, that it takes two years between each new burst of expansion (animals at a new site are one year old when they arrive; it takes one year for them to produce new offspring and a second year before these spread) and that the spread north started around 1850, the first 'stationary' roe deer could have reached Mälardalen around 1950. The first roe deer at our study sites in Västerbotten appeared around 1965. As this is another 600 km north of Mälardalen, there has not yet been enough time for animals of the 'stationary' type to reach this region. It is actually doubtful whether this part of Scandinavia will ever be invaded by the 'stationary' morph, as animals of this type may be unable to cross the large tracts of unsuitable habitat separating the isolated patches of favourable habitat.

If two distinct dispersal strategies do exist in roe deer, we should expect other cervids, similarly adapted to an unstable and unpredictable environment, to exhibit the same dimorphic dispersal pattern. In fact, they seem to do. In established populations of black-tailed deer *Odocoileus hemionus*, white-tailed deer *O. virginianus* and moose *Alces alces* dispersal patterns are similar to that of roe deer as observed in Mälardalen, with the majority of dispersers settling within a few home range diameters from their natal areas whereas a few travel very long distances (Bunnell & Harestad 1983, Nelson 1993, Sæther & Heim 1993). We believe this pattern is not just a mere coincidence, but instead it could be an effect of a dimorphism in dispersal behaviour, as outlined above, which conceivably occurs in species adapted to a patchy and unstable environment. Bunnell & Harestad (1983) actually speculated over the existence of two distinct types, 'non-dispersers' and 'dispersers', in order to explain the dispersal pattern exhibited by black-tailed deer. Unfortunately, we have been unable to find any reports on dispersal pattern in these other species in newly colonised areas.

Consequently, we hypothesise that the different dispersal patterns exhibited by roe deer in Västerbotten and Mälardalen are attributable to the existence of two genetically distinct morphs of roe deer, one 'dispersive' and one 'stationary'. We intend to test this hypothesis through a transplantation experiment in which juveniles from Mälardalen will be released in Västerbotten, and vice versa. Whatever the explanation for the observed pattern is, the results of the present study clearly demonstrate the danger of making broad generalisations from information obtained in one single study population only.

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