Seasonal migration pattern and home range of roe deer (*Capreolus capreolus*) in an altitudinal gradient in southern Norway

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Abstract

Seasonal migration pattern and home range of radio-collared roe deer (*Capreolus capreolus*) were studied in Lier, Norway, an area with a steep altitudinal gradient and a low population density of deer. Roe deer conformed to the usual pattern of temperate cervids with migration to low elevations during winter. Summer home-range size increased with increasing altitude, and only a small proportion of individuals had home ranges at high altitudes. It is concluded that these high elevation areas were probably of low quality. Time of spring migration was later in deer with a high elevation summer range. A lower frequency of females (30.0%) than males (61.5%) was stationary, and more females (30.0%) than males (0%) were long distance migrators (> 10 km). This supports an earlier hypothesis that migration patterns of roe deer are also influenced by social factors.

Key words: *Capreolus capreolus*, migration, home range, altitude

INTRODUCTION

Seasonal migration by large herbivores may be a strategy to enhance access to areas of high food abundance, quality and/or to reduce the risk of predation (Fryxell & Sinclair, 1988). Typically, migrating cervids in the temperate region choose a high elevation summer range and a low elevation winter range (elk, *Cervus elaphus canadensis*: Brazda, 1953; red deer, *Cervus e. elaphus*: Atzler, 1984; Albon & Langvatn, 1992; moose, *Alces alces*: LeResche, 1974; Pullainen, 1974; European roe deer, *Capreolus capreolus*: Robin, 1975; Mysterud, Bjørnsen & Østbye, 1997; Siberian roe deer, *Capreolus pygargus*: Danilkin, 1996; black-tailed deer, *Odocoileus hemionus*: Loft, Menke & Burton, 1984; Schoen & Kirchhoff, 1985). There is general agreement that the downhill migration in autumn/early winter is a strategy to find wintering areas with shallow snow depth (Nelson, 1995), because increasing snow depth lowers access to forage, increases costs of locomotion (Parker, Robbins & Hanley, 1984) and makes the deer more vulnerable to predation (Cederlund & Lindström, 1983). The mechanism explaining the subsequent uphill migration in spring is, however, less clear. Albon & Langvatn (1992) found that red deer with (coastal) summer ranges at high elevations were heavier than those with low elevation summer ranges during autumn. This suggested that the uphill migration is the result of the availability of better quality forage at high elevations, for which

they had some evidence. However, Hjeljord (1997) recently reported that (inland) moose at low elevations were heavier than those at high elevations during autumn. Evidently, the relationship between range quality, altitude and migration patterns of cervids needs further study.

Snow depth may not be the only factor affecting migration patterns of cervids. Female white-tailed deer have been reported to migrate further than males in some populations (Nelson & Mech, 1981; Nixon *et al.*, 1991), and Wahlström & Liberg (1995*a*) discovered that only female roe deer migrated (< 4 km), in two high density populations in Sweden. Snow depth can be assumed to induce similar migration patterns of males and females, at least for roe deer in which size dimorphy is minimal (Loison *et al.*, 1999). Migration was most evident in females without dependent young (Wahlström & Liberg, 1995*a*), which also precludes that long-distance migration of females serves to benefit their young which obviously have more problems in deep snow. Both these species, however, form small kin groups during winter when predation risk is high (Nelson & Mech, 1981; Wahlström & Liberg, 1995*a*). The present hypothesis to account for this pattern is, hence, that young females, which often disperse as yearlings (Wahlström & Liberg, 1995*a*,*b*), return to their mothers' range in order to minimize predation risk by joining a kin group, while dispersing males are more dominant and able to join a group at their new location

(Nelson & Mech, 1981; Wahlström & Liberg, 1995*a*). However, Bjar *et al.* (1991) found a tendency for females to be more often stationary than male roe deer in a medium density population in Østfold, Norway. This may be explained by the observation that winter group size increased and there was a reduction in the frequency of observations of solitary females of roe deer as density increased (Vincent *et al.*, 1995).

Detailed information about patterns of migration, such as frequency of migrators and distance and time of migration, is still limited regarding the European roe deer (Danilkin, 1996), and no study based on radio-telemetry has yet been conducted in areas with a steep altitudinal gradient (see Bjar *et al.*, 1991 and Wahlström & Liberg, 1995*a* for studies in flat terrain). I here present data on seasonal migration pattern and home range of radio-collared roe deer from a low density population in south-east Norway in an area with a steep altitudinal gradient. I test whether the uphill migration during spring is due to higher quality summer range at high elevation (Albon & Langvatn, 1992) or not (Hjeljord, 1997) by comparing summer home-range sizes at different altitudes. I test whether (Wahlström & Liberg, 1995*a*) or not (Bjar *et al.*, 1991) the frequency of migrators is higher in females than in males, and whether time of migration differs with sex, migration distance or elevation of the summer range. I also test whether internal home range use of roe deer differ between season and sex.

Study area

The study area is located in the Lier valley in southern Norway (between 59° 45′–60° 00′ N and 10° 05′–10° 20′ E). The topography is extremely hilly. On a coarse scale it rises from lake Holsfjorden at 63 m above sea level to above 600 m a.s.l. 1.5–2.5 km from the lake (Fig. 1). Then there is a high elevation forest plateau for 5–20 km to the next valley. Snow depth is typically deeper and more persistent at high elevation. Most of the area is forested and situated within the boreonemoral region (Abrahamsen *et al.*, 1977). Vegetation is varied. Along the bottom of the valley on richer soil, deciduous forest predominates, fragmented by small cultivated fields (Kjøstvedt, Mysterud & Østbye, 1998). In the deciduous forest, species such as hoary alder *Alnus incana* and bird cherry *Prunus padus* predominate mixed with elm *Ulmus glabra* and lime *Tilia cordata* on the richest sites. Above 200–250 m a.s.l. vegetation is dominated by Norway spruce *Picea abies* mixed with Scots pine *Pinus sylvestris* on the drier and poorer locations. Abundance of herbs is typically higher in the richer forest types which are situated mainly along the bottom of the valley than in the drier and poorer locations at high altitude (Mysterud, 1998*a*). The forest is commercially managed. Winter density of roe deer is about 3–5 deer per 100 ha (Mysterud, 1993). Red fox *Vulpes vulpes* and occasionally lynx *Felis lynx* are also found in the study area.

MATERIAL AND METHODS

During the 4 consecutive winters (February–March) 1994–1997 a total of 41 roe deer was captured in box traps or dropnets and fitted with radio-collars (Televilt Int. transmitters, TXE-3). Each individual was tracked by triangulation approximately every week for 1 year; after this, they were checked at more irregular intervals to see if they changed migration pattern. During summer and winter, more intensive tracking periods were conducted with radiofixes obtained at an average interval of 18 h (starting at 1000 h) from 1 to 25 March (1995–1997) and 1 to 25 July (1994–1997; later referred to as winter and summer range, respectively). Note that home range sizes for July 1994–1996 have been presented earlier in Mysterud (1998*b*), but only with a discussion of sexual differences in summer range size. Note also that 1 male and 1 female were followed from 1 June to 25 June 1995 with the same 18 h between observations, but range sizes were similar in June and July 1995.

Home-range sizes were estimated with the Minimum Convex Polygon method (MCP-100) (Mohr, 1947), the peeled MCP (MCP-95), excluding 5% of the observations most peripheral to the harmonic mean (Schoener, 1981) and the Kernel method (Worton, 1989) with the 90% isoline (Andreassen *et al.*, 1993). The RANGES IVm software package was used for all calculations. Autocorrelation was calculated with the Schoener index (Schoener, 1981; Swihart & Slade, 1985). Home range was regarded as the area an animal uses within a specific time period (Andreassen *et al.*, 1993), and autocorrelation as a descriptor of within home range movements (see Hansteen, Andreassen & Ims, 1997). A high compared to a low level of autocorrelation indicates that an animal either moves less or less directionally relative to range size within the given time frame. Because initial analysis showed some auto-correlation, I used estimates of home-range size from methods that are robust in this regard for further analysis (see above). I did this rather than increasing the time between observations, because autocorrelation does not decrease much beyond a certain limit (Hansteen *et al.*, 1997) and because comparable studies have used an even smaller time window (e.g. 6 h in Tufto, Andersen & Linnell, 1996).

I decided that an animal had migrated if summer and winter ranges did not overlap (MCP-95), and if the animal did not stay in the summer range for the next winter (i.e. returned to winter range, in contrast to dispersal with no return). Therefore, only data from individuals that were followed through at least one summer and one winter after capture were included. Migration distance was defined as distance between home range centres (harmonic mean). Date of migration during spring and autumn was the week in which the animal arrived at its summer and winter range, respectively. Altitudes were taken from maps (scale 1:5000) at the home range centres and at the position of the

Fig. 1. The location of the study area in Lier valley, Norway.

weekly fixes for migration patterns. Only adult animals (≥2 years) were included in tests, except in descriptive statistics of home range.

Statistical analyses

Home-range size variation (MCP-95 estimates, log-transformed), time of migration (week No.) and autocorrelation (Schoener index) were analysed with ANCOVA-models in the statistical package S-Plus (Venables & Ripley, 1994). Models were checked for assumptions of linearity, homogeneity of variance and statistically defined influence values (Cook's D; Venables & Ripley, 1994). Frequency of stationary, short and long distance migrators were analysed by the chi-square goodness-of-fit test (Bhattacharya & Johnsen, 1977).

Table 1. Home-range sizes of roe deer in Lier, southern Norway, during March (1995–1997) and July (1994–1997) estimated with the minimum convex polygon method (MCP-100), the peeled MCP (excluding 5% of the observations most peripheral to the harmonic mean, MCP-95), and the Kernel method using the 90% isocline (Kernel-90). All estimates are given as averages in ha ($\pm$ SE). Autocorrelation is measured with Schoeners index (see Methods). The juvenile age (juv) class is 9 months old in March and about 1 year old in July. Adults (ad) are at least 2 years old

Sex	Age	n	Period	MCP-100	MCP-95	Kernel-90	Autocorrelation
Males	ad	13	March	51.7 (6.7)	40.4 (6.4)	58.6 (10.4)	1.2 (0.2)
Males	ad	13	July	217.7 (84.4)	102.4 (22.9)	134.1 (29.3)	1.7 (0.1)
Males	juv	2	March	66.8 (30.9)	48.2 (17.5)	43.4 (11.7)	1.3 (0.3)
Males	juv	2	July	164.3 (66.5)	92.2 (2.0)	101.7 (34.7)	1.7 (0.5)
Females	ad	10	March	46.0 (13.4)	32.4 (8.4)	40.1 (9.5)	1.6 (0.1)
Females	ad	9	July	91.6 (40.2)	46.8 (12.2)	67.4 (21.6)	1.5 (0.2)
Females	juv	2	March	52.3 (0.5)	32.1 (0.6)	38.2 (2.5)	2.0 (0.7)
Females	juv	2	July	87.1 (5.4)	82.2 (7.7)	85.7 (7.2)	1.8 (0.1)

Table 2. The proportion (and absolute number) of stationary, short distance (< 10 km) and long distance migrating ($\geq$10 km) individuals among 23 radio-collared roe deer in the Lier valley, southern Norway during 1994–1997

Sex	n	Stationary	Short distance migration	Long distance migration
Females	10	30.0% (3)	40.0% (4)	30.0% (3)
Males	13	61.5% (8)	38.5% (5)	0

RESULTS

Altitude

Roe deer in Lier were recorded on average at higher elevations in summer than in winter, partly reflecting use of a wider range of altitudes during summer than in winter (Fig. 2). Only 15.4% ($n = 13$) of the males and 11.1% ($n = 9$) of the females had activity centres of summer home ranges above 300 m (Fig. 3), although high elevation areas constituted a large part of the study area (Fig. 1).
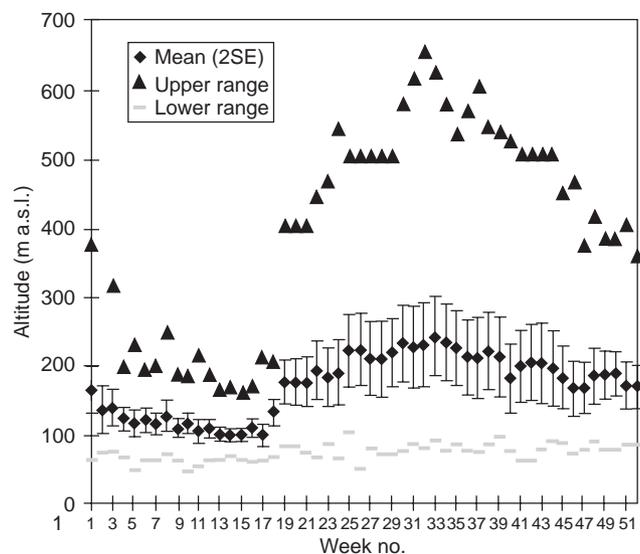

Fig. 2. Seasonal use by 22 radio-collared roe deer of an altitudinal gradient in the Lier valley, Norway, 1994–97.

Home range

Descriptive statistics of home-range sizes and autocorrelation are given in Table 1.

During summer, home-range sizes of adult roe deer increased with altitude (Fig. 3; ANCOVA; $n = 22$; $F = 20.761$; $P = 0.000$), and male range size was larger than female range size ($F = 9.480$; $P = 0.006$; see Mysterud, 1998b). There was no interaction between sex and altitude ($F = 2.020$; $P = 0.172$), i.e. the effect of altitude was similar for males and females.

Autocorrelation were not significantly affected by season (ANCOVA; $n = 45$; $F = 3.258$; $P = 0.079$), sex ($F = 0.004$; $P = 0.952$) or home-range size ($F = 1.036$; $P = 0.315$). However, there was interaction between season and home-range size ($F = 4.839$; $P = 0.034$), i.e. autocorrelation increased with increasing home-range size during winter only. There was also an interaction between season and sex ($F = 4.560$; $P = 0.039$), i.e. degree of autocorrelation was much higher during winter than summer for males only. There was no interaction between range size and sex ($F = 0.109$; $P = 0.744$). Removing one statistically defined outlier with a high Cook's D-value did not affect any factor notably.

Migration frequency and distances

The proportion of stationary, short distance (< 10 km) and long distance (> 10 km) migrators differed significantly between the sexes (Table 2; goodness-of-fit; $n = 23$; d.f. = 2; $\chi^2 = 8.218$; $P = 0.016$); fewer females were stationary and no males were long distance migrators. The average migration distance of males and females were 3.8 km (range 2.5–7.1 km) and 12.4 km
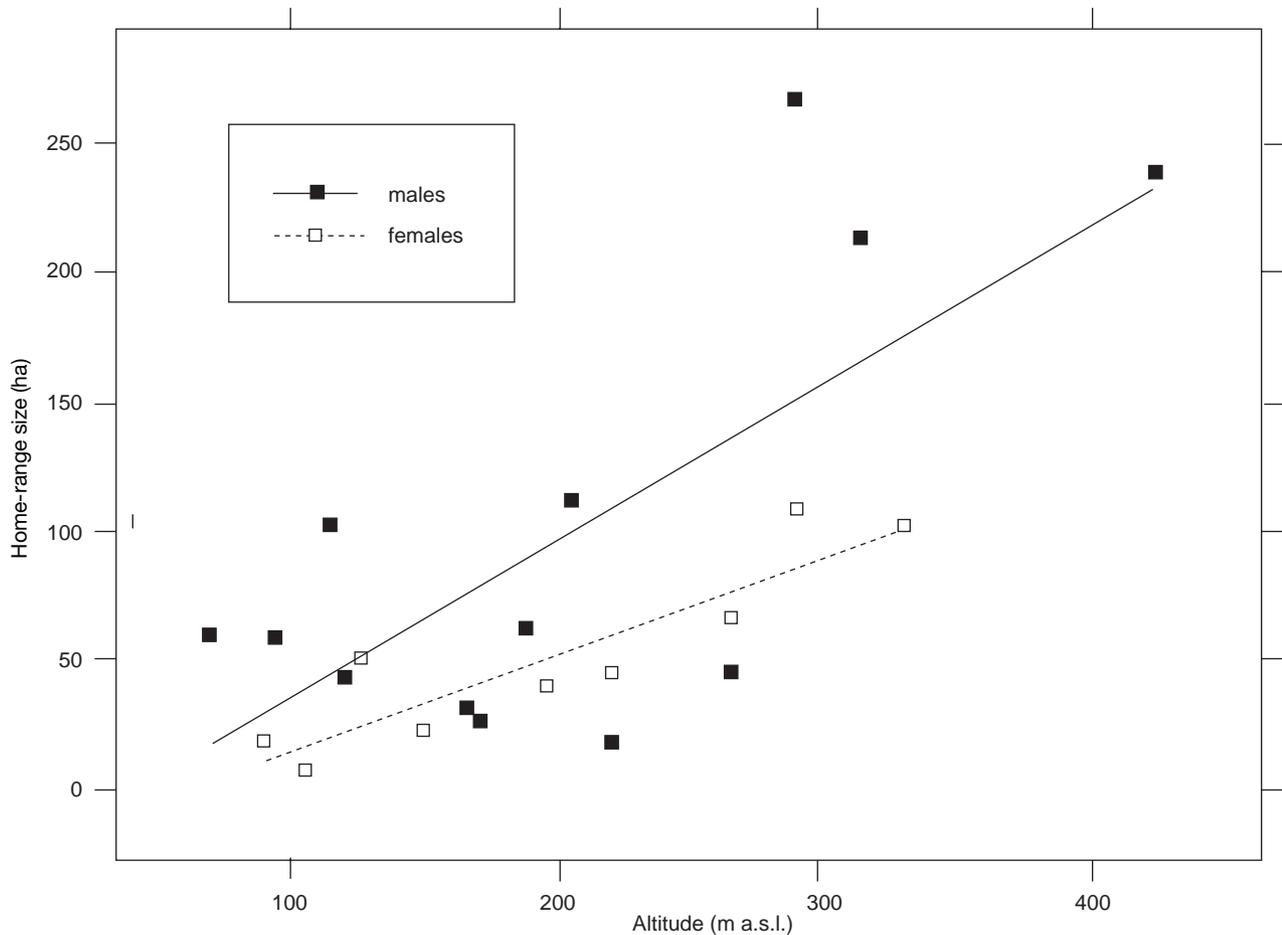
Fig. 3. Home-range size (MCP-95 estimates) of roe deer as a function of altitude in the Lier valley, Norway, during summer 1994–1997. Note that range size was log-transformed before analysis.

(range 0.7–45.7 km), respectively. One adult (likely a 2 year old) female moved 84 km, and remained in the new area. Another adult female settled in a summer range 18.1 km from the winter trap site after moving at least 40 km. She was poached in the new area before I could decide whether this was dispersal or migration.

All stationary animals remained stationary during successive years (three and two males followed respectively 2 and 3 years; one and three females followed respectively 2 and 3 years), whereas two deer changed from migration to being stationary (one male followed 2 years; one female followed 3 years). Three deer retained the migratory strategy (two females followed respectively 2 and 3 years; one male followed 3 years). One (2 year old) male changed both summer and winter range before being shot (3 year old).

Time of migration

Spring migration period was from first week of April to first week of June, averaging first week of May. Time of spring migrations were later for animals with summer home ranges at high than at low altitudes (Fig. 4; ANCOVA; $n = 12$; $F = 15.882$; $P = 0.007$), whereas

neither sex ($F = 3.120$; $P = 0.128$) nor migration distance ($F = 0.493$; $P = 0.509$) affected time of spring migration, nor did any of the interactions ($P > 0.1$).

Autumn migration period was from first week of September to third week of January, and averaged third week of November. Most deer migrated well in advance of a permanent snow cover, but the latest animals migrated typically when snow depth at high elevation exceeded 50 cm. Males tended to migrate earlier than females (ANCOVA; $n = 12$; $F = 5.157$; $P = 0.064$). Males and females migrated on average, respectively, last week of October and first week of December. There was no effect of altitude of summer ranges ($F = 0.414$; $P = 0.544$) nor migration distances ($F = 0.493$; $P = 0.509$) on time of autumn migrations, nor were there any interactions between these factors ($P > 0.5$).

DISCUSSION

Roe deer in Lier had, on average, summer ranges at a higher elevation than their winter ranges (Fig. 2), which is the typical pattern of migrating temperate cervids. However, the large summer ranges at high elevation (Fig. 3; see Loft *et al*., 1984 for a similar result on black-
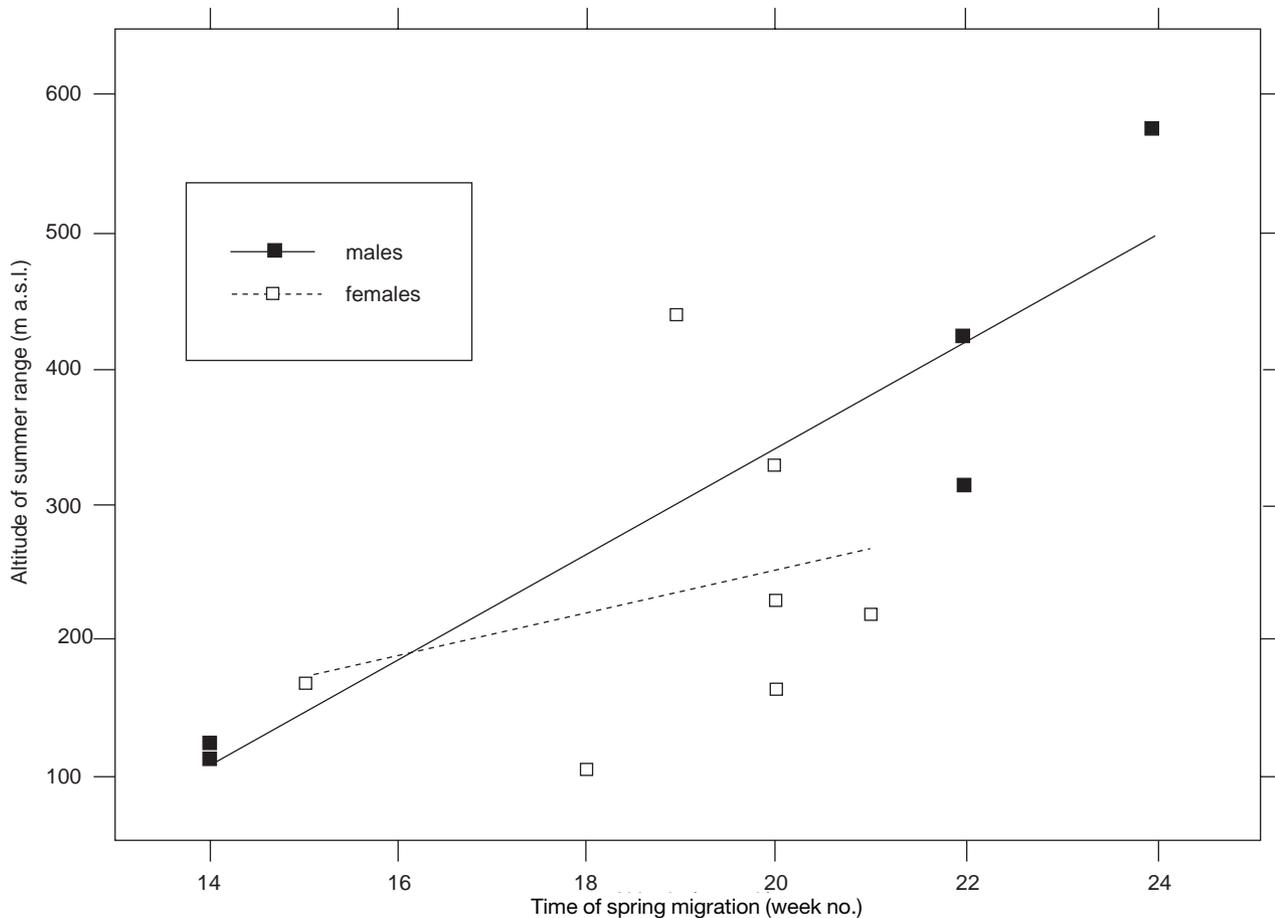
Fig. 4. Time of migration of roe deer in the Lier valley, Norway, during spring 1994–1997.

tailed deer), support the hypothesis that these areas are of low quality to roe deer, because the size of their home range during summer reflects resource levels (Wahlström & Kjellander, 1995; Tufto *et al.*, 1996). This is further evidenced by the low proportion of animals migrating to high elevations. Why then, move to high elevations during summer? Another possible hypothesis is that the use of high elevations is a result of density-dependent habitat selection (e.g. Fretwell & Lucas, 1970; Rosenzweig, 1981). High and low elevations may provide equal fitness even though range quality varies if deer density is also lower at high elevations. Alternatively, subdominant individuals are forced to high elevations by dominant individuals. There are at present no conclusive data to separate these two hypotheses, although Wahlström & Kjellander (1995) found that female roe deer at a landscape scale conformed to an ideal-free distribution in a flat terrain in Sweden.

Not surprisingly, roe deer with summer ranges at high elevations arrived later than those that migrated to a home range at low elevations (Fig. 4). It has been suggested that roe deer males should arrive in their summer range as soon as possible to get an edge in competition for a territory (Johansson, 1996), but I found no evidence that sex influenced time of spring migration in Lier. However, only two males at low elevation were migratory, and both of them arrived in

their summer ranges before the females (Fig. 4). It is therefore possible that there may be low competition for territories at high elevations.

No males migrated more than 10 km, whereas 30% of the females did. These females migrated much further than expected from local snow depth gradients, supporting the hypothesis that the contrasting patterns of migration for male and female roe deer are linked to their social organization (Wahlström & Liberg, 1995a). This was especially interesting since this was a low density population, a condition in which winter group size is reported to be small and a high frequency of the females are solitary (Vincent *et al.*, 1995). Several females were regularly or always seen alone in Lier, suggesting that other factors than grouping, such as familarity with range (Wahlström, 1995), may play a role. It is at present not known whether there are sex differences in spatial abilities (e.g. Gaulin & FitzGerald, 1986) in roe deer, or if this may act in concert with other factors.

The average migration distance of females (12.4 km) in Lier was about 10 times that in the two high density areas in Sweden (Wahlström & Liberg, 1995a), but estimates were closer to those from the medium density area in Østfold, Norway (10.6 and 6.6 km for females and males, respectively, but note that distances under 2 km were regarded as stationary; Bjar *et al.*, 1991). However, the frequency of migrating females was higher

in this study (for females and males, respectively, 70% and 39%, compared with 32% and 57% in Østfold, Bjar *et al.*, 1991). One extraordinary female in this study migrated 45.7 km in 3 consecutive years, accompanied by one calf the first year and two calves the next 2 years. Cederlund (1982) similarly reported a female with a calf migrating 40 km, while Cederlund & Liberg (1995) reported a lone female migrating 70 km. Long-distance dispersal, such as the female moving 84 km in this study, is common in the very low density populations in the northernmost part of Scandinavia where dispersal averaged 120 km among 17 yearlings (Wahlström & Liberg, 1995*b*).

Mode of home range use of roe deer in Lier varied between seasons for males but not for females, auto-correlation was much higher for bucks during winter than during summer. This makes sense since males defend a territory during summer (Strandgaard, 1972; Johansson, 1996), while home range use of females probably reflects the foraging pattern in both summer and winter. Autocorrelation increased with increasing range size during winter, but not during summer. This suggests that males with large ranges were able to patrol their territories as frequently as those with small ranges, at least with a time window of 18 h. Hence, auto-correlation as a measure of internal home range use (Hansteen *et al.*, 1997) shows promise.

Acknowledgements

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