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Chapter 6

Roe deer in northern environments: Physiology and behaviour

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INTRODUCTION

Over the last century roe deer have increased both their range and their densities throughout Europe. This expansion has been strongest in Fennoscandia, where a single remnant population in southern Sweden in 1850 has extended to cover much of Sweden, Norway and Finland (Cederlund and Liberg 1995; Olstad 1943; Pulliainen 1980; Raiby 1968; Wahlström and Liberg 1995a). Within this region they occupy a wide range of habitats, many of which differ greatly from the agricultural and deciduous forest habitats of central Europe where most research on roe deer has been conducted. While some of the southern and coastal areas of Norway and Sweden may provide patches of agricultural land with relatively little snow in winter, most of the Fennoscandia region is characterised by cold winters, short growing seasons, and high snow accumulation. As snow depth is widely believed to limit the northern distribution of roe deer (Danilkin 1989) these northern habitats must be regarded as particularly hostile to this short–legged ungulate. In addition, Fennoscandia supports the largest populations of lynx (*Lynx lynx*) in Europe (Breitenmoser and Breitenmoser–Würsten 1990), and lynx are a major predator of roe deer (Breitenmoser and Haller 1993; Aanes et al. this volume). How do roe deer survive in these extreme conditions? This chapter will examine two aspects of their survival strategy in the boreal forest regions of Scandinavia. Firstly, we will examine the ways in which roe deer physiology are adapted to maintaining homeostasis through the use of fat, and the regulation of energy metabolism, food intake and water balance. Secondly, we will examine the behavioural patterns of home range and habitat selection by roe deer during winter.

MORPHOLOGICAL AND PHYSIOLOGICAL ADAPTATIONS

In these extreme environments, animals are faced with numerous constraints, and morphological and physiological adaptations are clearly of crucial importance for their survival.

BODY SIZE

The two most important characteristics of animals that influence the cost of locomotion in snow are brisket height and foot loading. The roe deer's foot load is in the same range as for moose (*Alces alces*) and elk (*Cervus elaphus*) (Fancy and White 1985), whereas roe deer have the lowest brisket height of all northern cervids, indicating little tolerance of deep snow. At moderate to deep snow depths, when much of the field layer (ground vegetation) is already buried, the effect on energy expenditure becomes more important, especially at sinking depths near or greater than brisket height (Fancy and White 1985; Telfer and Kelsall 1984; Parker et al. 1984). Roe deer brisket height lies between 50 and 60 cms, and snow depths in many regions of Scandinavia can exceed one metre (Cederlund and Liberg 1995).

Critical temperatures for roe deer have not been reported, but Weiner's (1977) study of energy metabolism in roe deer suggests that the thermoneutral zone is between 17 and 26 °C in summer and somewhat lower in winter, at least under continental conditions. Large animals loose less heat relative to body weight than smaller ones. Large size may therefore be an adaptation for energy conservation, especially in continental areas with relatively deep snow and cold winters. Further, nutrient requirements are allometrically related to body size, while gut capacity is isometric with body size. Larger bodied ruminants are therefore somewhat less constrained by energy requirements: hence they have the opportunity to increase retention time of digesta in the alimentary tract and, as a consequence, the digestibility of the food. Smaller ruminants like roe deer are therefore more dependent on access to a high quality diet than are larger ruminants.

Increased body size will therefore reduce the energy cost of walking in snow, reduce thermal stress during cold, allow for a disproportionate increase in fat reserves and assist in tolerating the nutrient dilution accompanying a highly fibrous diet. All these factors increase in importance along a latitudinal gradient from the south to the north, which may explain the general trend for body weight of roe deer to increase in parallel (Danilkin and Hewison 1996; Andersen et al. this volume). However, there are many exceptions to this trend in body size (Cederlund and Liberg 1995), for which there are at least three possible explanations. First, selection for increased body size as a response to climatic factors has not been powerful; secondly, that it has not been at work for a long time; or, thirdly, that it is counterbalanced by other selective forces like food shortage (Langvatn and Albon 1986).

PELAGE

In order to minimise heat loss as temperatures decline, animals may adjust their thermal resistance. The conductive properties of the pelage play an important role here: for temperate ungulates, pelage conductance in winter is around half that in summer (Parker and Robbins 1985). The same is probably true for roe deer where pronounced seasonal differences in length and architecture of the hair have been reported (Johnsen and Hornby 1975). However, increased insulation will also reduce the upper critical temperature. Consequently there is a trade off on how thick the winter coat should grow, depending on the changes in seasonal temperature and amplitude of temperature shifts during winter. Roe deer have a lower density of hair than the larger moose, which may indicate that selection for thick pelage and increased body size has not been at work for long (see above). Other general physiological mechanisms influencing thermal resistance working on a finer time scale (i.e. counter–current heat exchange, differential blood flow to extremities, vasomotor control of skin and tissue temperatures, changes in evaporation and cutaneous water loss) may modify this situation, but these have not been examined in detail for roe deer.

FAT RESERVES

The 2–3 fold increase in the digestive energy intake by northern ungulates in summer as compared to winter, underlines the importance of nutrient storage to compensate for the discrepancy between nutrient intake and requirements in winter. A latitudinal increase in capacity of storing fat, compensating for lower forage availability and a longer period of low quality forages could be anticipated. Based on scattered data of body composition and indirect indices, the maximum fat reserves in roe deer seems to be lower in Britain and continental Europe (Weiner 1973; Hoffmann 1977; Loudon 1987; Hewison et al. 1996) than in Fennoscandia (Holand 1992a) where reserves can reach 2.5 kg, or c.10% of body weight (Holand 1990).

The lower threshold of body fat for survival in roe deer, based on body composition of starved roe deer, is around 1.5% on a dry matter basis (Holand unpublished data). Compared to adults, fawns have lower reserves in the fall (Table 1) because of higher metabolic rate and locomotion cost per kilo body weight. Fawns are therefore more susceptible to winter starvation than adults. The body composition and weight of starved animals indicated a complete depletion of all catabolizable fat reserves and an estimated 20% reduction of total protein reserves in adults, with even more in fawns. Holand (1990) calculated that fat and protein reserves may at most cover 20% of the TEE (total energy expenditure) during a 3 month period of negative energy balance. Hence, the principal source of energy in winter

Table 6.1 Fat content expressed as percentage of ingesta–free body weight (IFBW, in kg) of European roe deer in relation to season in southern Norway.

	Summer	Late fall	Winter	Late winter
Does	(n=7)	(n=6)	(n=3)	(n=5)
IFBW	22.1±3.8a*	23.6±2.3a	22.4±0.9a	20.2±2.2a
Fat	3.5±1.0b	9.2±1.0a	3.4±0.8b	1.9±0.6b
Bucks	(n=8)	(n=7)	(n=3)	(n=4)
IFBW	24.4±2.5a	26.6±4.3a	22.0±1.2b	21.7±1.9b
Fat	4.5±1.1b	10.3±2.1a	3.8±1.1bc	1.7±0.9c
Fawns		(n=7)	(n=4)	(n=5)
IFBW		17.1±2.9a	15.2±2.7ab	12.6±2.1b
Fat		5.1±0.8a	2.3±0.5b	1.6±0.4b

Note: Values are given in means ± standard deviation. Parameters in the same row followed by the same letter are not significantly different.

for roe deer is their food supply rather than stored reserves, indicating the importance of nutritional and behavioural adaptations to winter conditions.

FAT RESERVES AND REPRODUCTIVE STRATEGY

Foraging, predator avoidance, storing fat, and growth cannot be dealt with usefully in isolation since they usually make conflicting demands on limited resources, which leads to resource allocation strategies in the animals. Fat storage should therefore be viewed in the context of how it will influence reproduction as well as survival.

The intersexual similarities in fat cyclicity and amplitude (Table 6.1) in roe deer contrast with the patterns in all other northern cervids and reflect inter–specific differences in reproductive strategies. The mid–summer rut of roe deer follows immediately the period of peak lactation, leading to synchronisation of reproductive effort between the sexes (Sempéré et al. this volume, Liberg et al. this volume). This enables the adults of both sexes to replenish their body reserves in fall and meet the winter with maximum fat reserves. Delayed implantation (embryonic diapause), allows the energy costs of mating behaviour to be met in summer rather than in mid–winter (Sempéré et al. this volume) when dietary energy is at its lowest.

NUTRITIONAL ADAPTATION

The seasonal variations in nutrition are a continuum, in quantity and quality, with at one extreme the summer, when forage is accessible, abundant and of high quality. At the other end is winter, with heavy snow, low forage availability and quality, and increased search costs (see above). The trade–off between diet quality and quantity exists at all points on the curve illustrating the nutritional constraints facing animals living in this environment. The processing strategy of the forage must further be linked with the function and morphology of the digestive tract to understand how the animal alters its feeding behaviour to exploit its seasonal environment.

In coniferous forests, snow depths of about 50 cm restrict access to the best quality winter forage, such as bilberry stems (*Vaccinium myrtillus*, see below), it thereby induces a reduction in diet quality. This is reflected in the higher cell wall fractions (especially lignin) of the diet, measured as chemical composition of rumen content, in winter than in summer (Table 6.2). This shift in diet quality was accompanied by an increase in dry matter

Table 6.2. Chemical composition of rumen contents of roe deer (g / 100g dry matter, data from Holand 1992b). Values are given as means ± SD. Values in a row followed by the same letter are not significantly different at the P < 0.05 level.

	Percentage of dry matter			
	Winter n = 9	Late winter n = 19	Summer n = 24	Autumn n = 12
Hemicellulose	16.7 ± 2.3a	16.1 ±1.2a	12.6 ± 2.2b	16.5 ±2.1 ab
Cellulose	20.2 ± 3.8a	18.1 ± 2.9b	12.2 ± 2.6 c	17.5 ± 2.5b
Lignin	18.1 ±2.4ab	16.7 ± 1.5a	7.1 ± 2.5c	12.7 ± 3.4b
Cell wall	55.0 ±3.6a	50.9 ± 2.3b	31.9 ± 3.0d	46.7 ± 2.9c

Table 6.3 Seasonal variation in rumen capacity (volume, l) and the utilization ratio (rumen contents (wet weight, kg)/rumen capacity) in roe deer (data from Holand 1992b). Values are given as means ± SD. Values in a row followed by the same letter are not significantly different at the P < 0.05 level.

	Winter n = 8	Late winter n = 19	Summer n = 24	Autumn n = 12
Rumen capacity	3.7 ±1.0a	4.2 ±0.8a	4.3 ±0.8a	4.0 ±0.8a
Utilization ratio	0.52 ±0.13a	0.48 ±0.11ab	0.34 ±0.08c	0.40 ±0.09bc

content of the rumen–reticulum and the distal fermentation chamber (Holand 1992b). A higher rumen fill in relation to rumen capacity (Table 6.3) indicated that roe deer have the capacity to buffer the low digestible forage by increasing fill. However, the rumen cellulolytic activity seems low both in summer and winter (Holand 1993; Deutsch et al. submitted.), which may indicate a rumen bulk limitation in winter. Consequently, voluntary intake would be greatly restricted on a typical winter diet of shrubs and browse (Holand 1992b, Holand 1994a).

The digestibility of a ruminant diet is determined by ruminal retention and turnover. Digestive kinetic studies in roe deer showed a much shorter mean retention time of the ingesta on a concentrate diet with small particle sizes and high quality, than on a low quality diet (Table 6.4). When fed a

Table 6.4 Digestive dynamics, expressed as total mean retention time (TMRT) and rumen retention time (RRT), based on estimates using a particulate marker (141Ce), of roe deer fed high and low quality diets (concentrates and bilberry, Vaccinium) ad libitum and restricted in winter and summer (data from Holand 1994a). Values are given as means ± SD. Values in a column followed by the same letter are not significantly different at the P < 0.05 level.

	Body weight (kg)	Food intake (g/bw$^{0.75}$/ day)	TMRT (h)	RRT (h)	Apparent digest. (% of DM)
Winter					
Bilberry stems					
Ad libitum	24.8 ± 3.4a	36.9 ± 2.8c	31.1 ± 2.6b	15.5 ±1.4ab	54.2 ±2.9c
Restricted	24.4 ±3.6a	24.0	36.7 ± 2.3a	22.1 ±5.9c	51.9 ±4.1c
Concentrate					
Ad libitum	24.3 ±1.8a	47.9 ±7.2b	24.2 ± 1.3c	13.1 ±2.1b	87.1 ±2.7a
Restricted	24.4 ±3.5a	34.0	19.4 ±3.6cd	12.2 ±1.4b	79.3 ±5.3b
Summer					
Bilberry stems					
Ad libitum	25.2 ± 2.8a	34.0 ±3.5c	30.6 ±2.6b	19.1 ±2.8a	52.2 ±8.8c
Restricted	25.0 ±3.2a	24.0	36.2 ±2.3a	22.1 ±5.9a	52.7 ±7.3c
Concentrate					
Ad libitum	24.8 ±3.4a	57.6 ±2.4a	19.6 ±2.0d	8.7 ±1.9c	86.7 ±3.6a
Restricted	24.9 ±3.2a	34.0	18.8 ±3.0d	12.4 ±1.3b	77.4 ±6.3b

restricted ration of *Vaccinium*, the retention time increased even more, but the digestibility did not improve (Table 6.4). This indicates that increased rumen retention is not an effective means of increasing cell wall digestion in roe deer. Passage of undigested residues (mainly lignin and cell wall content) is dependent upon the rate of physical breakdown which is primarily a function of rumination time. Roe deer feeding on a *Vaccinium* diet, ruminated for 8 hours per day (i.e. longer than on less fibrous foods, Holand unpublished data). Thus, increased rumination can to some extent compensate for the longer retention time of high fibre diets (see Table 6.4). Finally, Hofmann (1989) and Holand and Staaland (1995) suggested that enhanced distal fermentation in winter could favour winter survival in roe deer. However, Deutsch et al. (submitted) reported low cellulolytic activity in the distal fermentation chamber (the hindgut), so this mechanism is unlikely to be important.

Although roe deer are bulk–limited in winter, browse is then their staple food. As snow depth influences locomotion cost a selective feeding strategy in winter may be uneconomic (see below). Under extreme snow conditions roe deer are therefore more likely to be constrained by acquisition of forage rather than by rumen fill. Hence, the "extreme" winter digestive strategy may be to collect enough forage and to increase rumen retention time sufficiently to keep as viable and stable a rumen environment as possible.

METABOLIC RATE

Hudson and Christopherson (1985) pointed out that high metabolic rates are expected in species exploiting strongly pulsed forage resources. Animals living in such environments must grow and fatten rapidly during a short growing season leading to strong selection for a seasonal rhythm of metabolic rate, connected to the growing season. Hudson and Christopherson (1985) also pointed out that the highest metabolic rates among herbivores are found in northern Cervidae. Reduced energy metabolism in winter has been reported in several northern ruminants (see Mauget et al. 1997 for a review). Weiner (1977) did find seasonal variation in the fasting heat production of roe deer, although the variation was rather small, of the order of 10%. However, further studies failed to find evidence for any significant seasonal cycle in metabolic rate among male or female roe deer from France, apart from those associated with gestation and lactation (Mauget et al. 1997). If this endogenous cycle is also lacking in northern roe deer, living in a more seasonal environment, it implies that the species is unique among northern cervids. Alternatively, if an endogenous cycle is present in northern roe deer it will provide strong evidence for geographical variation in selection for metabolic activity.

WATER METABOLISM

Low water turnover, especially in winter (Table 6.5), indicates an effective kidney function and reabsorption mechanisms for water in the large intestine (Holand and Staaland 1995). The water requirement is closely related to the protein intake and ambient temperature (Holand unpublished data). Given an estimated water requirement of 70 ml/(kg body mass)$^{0.75}$ per day and an ambient temperature of −20 °C, it will cost about 35 KJ/(kg body mass)$^{0.75}$ per day to melt the snow and to raise the water temperature to that of the body. This energy cost amounts to about 10% of the winter basal metabolism of roe deer based on Weiner's (1977) data. Compared to the estimated energy expenditure of locomotion in snow of northern ungulates, which can easily amount to 100% of winter basal metabolism (Parker 1983; Fancy and White 1985) the energy cost of an adequate water balance is small.

Table 6.5 Water transfer rates, WTR (ml/(kg body weight)$^{0.75}$ per day) and crude protein intake, CPI (g/kg body weight)$^{0.75}$ per day) of roe deer fed 3 different diets at 3 different temperature ranges (data from Holand unpublished). Values are given as means ± SD. WTR values followed by the same letter are not significantly different at the P <0.05 level.

	Concentrate		Grass pellets		Oats	
Temperature	WTR	CPI	WTR	CPI	WTR	CPI
Cold −5.6 to −3.2°C	210 ±33d	17.3±1.8c	160±16c	10.9±1.0b	85±8a	6.6±1.7a
Moderate 3.0 to 4.4 °C	191 ±50cd	13.6±2.6bc	210±12d	11.1±1.5bc	102±13ab	4.3±1.4a
Warm 17 to 19.4 °C	266 ±57d	20.9±7.0c	228±13d	14.0±1.5c	125±10b	10.9±1.5b

Based on estimated fat and protein reserves of roe deer in late fall (Holand 1992) and a total possible loss of 20% of body mass through winter (Holand unpublished data), metabolized water may at best account for 5% of daily water requirement. Metabolized water is therefore of minor importance for the water budget throughout winter, and snow will be the main water resource. It is known that roe deer can survive with snow as their only source of water (Holand unpublished data).

MINERAL BALANCE

A wide range of good food resources available in summer compared to the low forage quality, diversity and availability in winter, can affect the mineral regime of ungulates. There may be a build-up of mineral stores in summer and a depletion in winter, as occurs for fat (Holand 1994b), reflecting the high nutrient concentration in the summer vegetation. However, seasonal differences in body pools are rather small (Holand 1994b) and the mineral levels of starved animals in winter are in the same range as for culled animals, indicating no severe mineral depletion in winter (Holand unpublished data). This is confirmed by the effective mineral absorption mechanism in roe deer (Figure 6.1). Large quantities of minerals are absorbed from the small intestine, and the caecum, while the proximal colon also plays an important role. This underlines the importance of the hindgut in roe deer not only for digestion of energy and protein, but also for the conservation and absorption of important minerals. The absorption processes are facilitated by a slow turnover of the ingesta, as seen in winter, and an increase in the surface area for absorption. Small amounts of several minerals are also absorbed from the coiled and distal colon; these are important to maintain the mineral balance in roe deer, especially the Na balance since the daily intake of sodium is in the order of 10mM or less. Mineral deficiencies may be expected in interior areas with relatively lower mineral levels in the vegetation. However, the influence of marine aerosol is strong in most of Fennoscandia and so far we have no indication that mineral deficiency influences growth or reproduction.
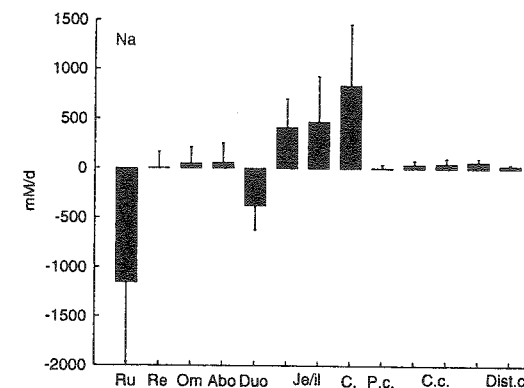

Figure 6.1 Absorption or secretion of sodium in the alimentary tract of the roe deer. Columns below abscissa indicate secretion into the alimentary tract and those above absorption from the alimentary tract. Mean and 1 SD are shown. (Data from Holand and Staaland 1995).

BEHAVIOURAL STRATEGIES FOR WINTER SURVIVAL

The winter period with an increased demand of energy for maintenance coincides with a period of low availability and quality of forage. Roe deer have limited fat reserves and face severe physiological constraints on digestion of the most common winter forage (see above): though they show reduced activity under deep snow conditions (Cederlund 1982; Thor 1990), they must feed, so behavioural plasticity may be subject to strict energy/time constraints (see Schmitz 1991 for a discussion of these issues in white–tailed deer *Odocoileus virginianus*). From a theoretical point of view herbivores can buffer the effect of low quality environments by allocating additional time to search for the highest quality forage available. However, in northern areas where snow accumulates during winter, the energetic costs of locomotion, and, therefore, search costs of foraging, increase sharply, especially when snow depth exceeds brisket height (see above). Under these circumstances the nutritional strategy may shift from one of maximising energy intake (during summer), to a trade–off between maximising intake and minimising energy expenditure during winter. Vulnerability to predation also increases during periods of deep snow (Cederlund and Lindström 1983). Behavioural adaptations and habitat selection that allow the individual to avoid moving in areas with deep snow are therefore likely to be especially important.

Different factors influence selection and movement patterns of herbivores at different spatial scales (Senft et al. 1987). When viewed as a hierarchy, habitat selection may transcend such diverse behavioural processes as food selection, patch selection, dispersal and migration (Schaefer and Messier 1995). In this section, we describe how roe deer select their winter home ranges within a region, and how they use the different habitats for foraging and resting within this home range.

SELECTION OF WINTER HOME RANGE

Snow accumulation and consistency are modified by habitat, altitude, topography (Beier and McCullough 1990) and distance from the ocean. There is generally less snow on steep slopes (Reitan 1988), at low altitudes and in habitats with good canopy cover (Eide 1995; Mysterud et al. 1997). In areas of coastal Norway and southern Sweden where snow rarely accumulates, roe deer are usually dispersed throughout available habitat (Wahlström and Kjellander 1995) and use the same home range all the year round, or at most make short local movements between summer and winter areas (Andersen et al. 1995; Wahlström and Liberg 1995b; Table 6.6). However, in the interior boreal forest areas, winter snow depth often

Table 6.6 Seasonal migration distances (n) of roe deer in different areas of Norway (N) and Sweden (S) with different snow regimes.

Study site	Snow	Migration Distances	Reference
Storfosna (N)	Shallow	0.5 km for adult males (46) 0.4 km for adult females (63)	Andersen et al. 1995
Ekenäs (S)	Shallow	1.8 km for females (8)	Wahlström and Liberg 1995b
Bogesund (S)	Shallow	3.8 km for females (3)	Wahlström and Liberg 1995b
Ås (N)	Medium	58 % stationary (19) 42 % moved an average of 8 km (14)	Bjar et al. 1991
Lier (N)	Medium	30 % stationary females (3) 62 % stationary males (8) 70 % females moved 12,4 km (7) 39 % males moved 3.8 km (5)	Mysterud 1998
Västerbotten (S)	Deep	61 % stationary (11) 22 % migration < 5km (4) 17 % migration > 5km (3)	Cederlund and Liberg 1995
Hedmark (N)	Deep	3 km for males (15) 7 km for females (12)	Linnell et al. 1996

reaches 1 m in open areas (Cederlund 1982). It is therefore not surprising that in areas where snow depth gradients exist, roe deer move to the valley bottoms in late autumn and remain there until spring (Cederlund and Liberg 1995; Eide 1995; Linnell et al. 1996; Mysterud et al. 1997; Mysterud 1998). In other areas where local gradients in snow depth do not exist, roe deer remain year round within the same region (Cederlund 1983), and exploit local topographic features and habitat types (such as cliffs, Reitan 1988), although in years with particularly high snowfall they suffer here high mortality due to starvation and predation (Borg 1970;

1991, Cederlund and Lindström 1983). None of these winter strategies are really analogous to the winter deer–yards formed by northern populations of white–tailed deer (Messier and Barrette 1985), as the roe deer remain as dispersed as possible throughout the winter areas, or at most form small groups (<10 animals) that occupy pockets of suitable habitat.

Although many individuals in boreal habitats remain in the same home range year–round, a large proportion use separate summer and winter areas and make seasonal migrations between the two ranges (Table 6.6). These migrations, generally <10 km, are not like the mass migrations of Siberian roe deer (Capreolus pygargus) reported by Danilkin and Hewison (1996) and Danilkin et al. (1993); they exploit smaller local vertical and horizontal snow depth gradients (Table 6.6). The result is that summer ranges are much more dispersed than winter ranges. Females sometimes migrate further than males (Table 6.6), perhaps because of different patterns of grouping: yearling females that leave their natal range during early summer are subdominant in their new area and hence move back to their mother during autumn when the formation of groups begins, whereas young males have higher social status and are allowed to become a part of the winter group in the new area (Wahlström and Liberg 1995b, Linnell et al. this volume). These migrations therefore often terminate when the female forms a new clan with her own fawns, but in some cases the migration pattern seems to last (Mysterud 1998). One other feature associated with these boreal habitats is a very high natal dispersal rate (Linnell et al. 1996, Wahlström and Liberg 1995b; Linnell et al. this volume) and a reduced fidelity to seasonal home ranges among adults (Linnell unpublished). The result of these movement patterns is that roe deer populations of boreal forests are much more mobile than most other western European populations.

A common management measure throughout the Fennoscandia region is the provisioning of extra food for roe deer during winter at artificial feeding sites in an attempt to improve winter survival (Kjøstvedt and Holand 1997). In areas with deep snow, roe deer seem to become quite dependent on artificial feeding which influences both home range location, and habitat selection within the home range. In one snow–rich Norwegian study site (Hedmark), no tracks of roe deer were found at more than 2 km from a feeding site, and 82% of all tracks were within 800 m of a feeding site. The attraction of these feeding sites led to a high degree of clumping of the population, not only vertically (at the valley bottoms), but also horizontally (along the valley bottom) (Eide 1995; Wannag 1997). This clumping of roe deer provides a very stable and predictable food resource for lynx, that prey heavily on them, travelling from one feeding site to the next. As most feeding sites are located near houses, roe deer are also vulnerable to predation by loose dogs (Linnell et al. 1996). In the Hedmark study area an average of 4–5 roe deer were found at each site (Linnell et al. 1996). These animals behaved as virtually a single social unit staying on average within 200 m of the feeding site (Linnell et al. 1996; Wannag 1997). Home ranges varied from 20 to 100 ha with a single core area concentrated around the feeding site. Similar results were obtained from two study populations in Sweden, where roe deer also concentrated their activity within 50–100 ha around feeding sites (Cederlund 1983; Guillet et al. 1996) despite there being less snow present than in Norway.

USE OF HABITATS WITHIN WINTER HOME RANGE

The pattern of habitat selection within a winter home range may result from a strategy of maximising net energy gain (high food intakes and low energy expenditures; see Schmitz 1991 for a comparison with the winter survival strategies of the larger white–tailed deer). The main food source of roe deer during winter has generally been found to be various species of Vaccinium from the field layer, especially bilberry (Vaccinium myrtillus) (Cederlund et al. 1980; Mysterud et al. 1997). However, as there appears to be a maximum depth beyond which it is uneconomical to dig craters (Mysterud et al. 1997), or when the field layer is made unavailable by crust formation, species from the shrub layer, like rowan (Sorbus aucuparia), birch (Betula sp.) and arboreal lichens, are used more (Helle 1980; Mysterud and Østbye 1995b). In winter areas with little snow, relatively open habitats such as young plantations and agricultural crops were preferred for foraging (Andersen et al. 1995; Guillet et al. 1995; Mysterud and Østbye 1995a). As snow depth increases, these open habitats are used less, and older age stands, with less snow, are selected (Mysterud et al. 1997). The results of this change in habitat selection can also be seen in movement patterns: in one study, as snow depth increased the distance travelled each day decreased (i.e. roe deer remained within mature forest patches), but overall during periods of deep snow accumulation they used larger home ranges (i.e. more patches) and moved to artificial feeding sites (Cederlund 1982, 1983; see above). At artificial feeding sites in Hedmark, the area used was smallest in mid–winter when snow depth was at its greatest, but rapidly increased as snow began melting in April (Wannag 1997). Activity at feeding sites in Sweden was also more concentrated at sites with deeper snow (Guillet et al. 1996).

Apart from the obviously important influence of the quantity and quality of the food resource for selection of feeding sites by cervids, habitat structure (cover) has a strong influence on selection of bedding sites (Armstrong et al. 1983; Mysterud and Østbye 1995a). Cervids typically have an alter-

nating foraging–resting–foraging activity pattern. Roe deer rest (including rumination time) for about 60% of the time during the winter season divided between about 8 bouts (Cederlund 1981, 1989; Jeppesen 1989). Cover may be especially important at northern latitudes due to (1) its ability to moderate thermal extremes (Moen 1973), and (2) the lower risk of predation since visual detection is less likely, and cover may obstruct predators (Messier and Barrette 1985; Peek et al. 1982). During summer, roe deer can usually select habitats that provide a suitable combination of both food and cover (Mysterud 1996; Tufto et al. 1996), whereas during winter the distribution of accessible resources changes so that a trade off between selection of food and cover can regularly arise (Mysterud and Østbye 1995a). Why then, do roe deer often choose to move to cover when selecting a bed–site during winter?

During a snow–poor winter in a forested area in Buskerud, southern Norway, roe deer were found to forage mostly in open habitats such as small agricultural fields, deciduous forest and clear–cuts (Mysterud and Østbye 1995a). As would be expected if they were trying to reduce heat loss through radiation and convection from wind, there was more canopy cover at bed–sites than at random sites, and beds were often situated close to a spruce tree. However, there were also many bed–sites in open habitats close to the feeding sites (Figure 6.2). Distance from feeding site to bed–site

Figure 6.3 The relationship of both bedding duration and temperature to canopy cover over beds was significant. S, short stay; L, long stay; M, mild period; C, cold period (See Figure 6.2 for details, from Mysterud and Østbye 1995 a).

varied from 0 to over 200 m, most bed–sites were close to feeding sites, however, when bedding for long periods and in colder weather, the deer sought more cover (Figure 6.3). Temperature had no effect on the use of feeding sites, so seeking cover for bedding required moving further away from the feeding sites. The effect of temperature and wind–chill were not separated, but roe deer had more ground cover in the direction of incoming wind, suggesting that wind–chill was an important part of the thermal environment (Mysterud and Østbye 1995a). This implies that when bedding for longer periods between foraging bouts, roe deer were more selective about choosing bed–sites that afforded thermal benefits than when bedding for short periods.

It is difficult to assess to what degree the use of cover is influenced by predation risk since this is not easily quantified. However, roe deer bed–sites are well hidden compared to random plots, and suggests that they seek cover to lower the chance of visual detection (Mysterud and Østbye 1995a). There was rather little variation in degree of ground cover (i.e. sighting distance or visibility) at bed–sites in the Buskerud study area, suggesting that roe deer seldom bedded in areas with little ground cover although such areas were available (Mysterud and Østbye 1995a). We conclude that thermal factors (especially the combination of low temperature and wind) affect the use of cover, but that patches of cover need not be large to be effective thermal protection.
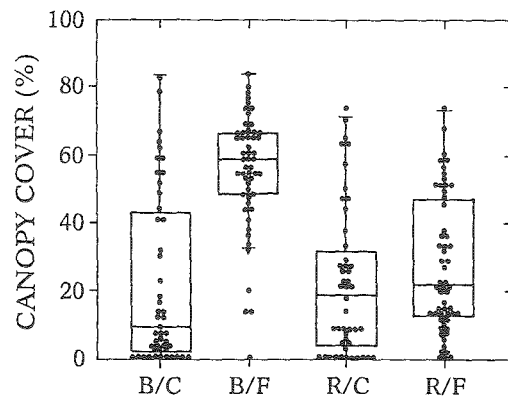

Figure 6.2 Differences in canopy cover for beds situated near to (B/C) and far (B/F) from feeding sites. Canopy closure was significantly higher for B/F than for the random points (R/F), whereas B/C did not have a significantly different canopy closure from the random points (R/C). The horizontal lines in the boxes represent that median and the upper and lower quartiles. The vertical lines above and below the box show 1.5 times the distance between the median and the upper and lower quartiles (from Mysterud and Østbye 1995 a).
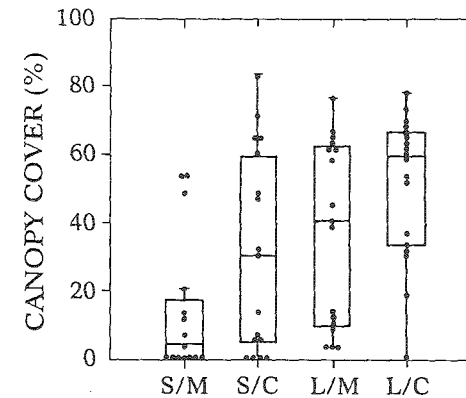
CONCLUSIONS

Their heavy foot loading, small body size, and low brisket height are among factors that present challenges to roe deer in northern environments. Nevertheless, roe deer have expanded their range in Scandinavia in recent decades and occupy many areas that have severely cold winters with deep snow. Based on this review, we expect that thermal factors are less important for the energy budget of roe deer than nutrition and disturbance (where this causes costly movements, Moen 1968). Unlike many other northern ungulates which have large fat deposits the roe deer's meagre fat reserves can supply only about 20% of their winter energy needs, the remainder of their energy must come from their daily food intake. Furthermore, it appears that roe deer are bulk limited when it comes to digestion during winter. In forest areas they rely on Vaccinnium as their staple winter food, but snow depths greater than 50 cm limit roe deer access to this food. Energy expenditures for winter foraging can reach 100% of maintenance costs, so avoiding the costs of additional movements in deep snow are particularly important to foraging roe deer.

During winter roe deer are often quite evenly dispersed in areas with little snow accumulation, but in areas with deep snow, roe deer congregate in areas where local topographic features (cliffs, valley bottoms, dense forests) or artificial feeding allows roe deer to obtain food while minimising the high costs of locomotion in deep snow. Because of their small size and low absolute energy requirements roe deer are able to survive in fairly small pockets of suitable habitat during winter, an advantage that further reduces their use of energy on locomotion. Cover seems to be particularly important for selection of winter bed–sites and the influence of such cover increases with the duration of bedding and with decreasing temperature.

Apart from our lack of information on the role of predation risk in affecting the costs and benefits of winter behaviour patterns, both the physiological and behavioural aspects of the winter survival strategy of roe deer are relatively well understood. Comparative data from southern regions are lacking. How do roe deer survive in the hot and dry environments of southern Spain and Italy ? Further physiological and behavioural investigations are clearly needed to determine how roe deer survive in these other extremes of climate.

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