

Effects of Severe Winters and Fox Predation on Roe Deer Mortality

Göran CEDERLUND & Erik LINDSTRÖM

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This is a study of the mutual impact of roe deer, *Capreolus capreolus* (Linnaeus, 1758) and red foxes, *Vulpes vulpes* (Linnaeus, 1758); deer mortality and food supply needed for fox reproduction. Density of roe deer was reported via questionnaires to increase during the study except an interruption after the severe winter 1976/77. The interruption was more pronounced in a northern forested area with deeper snow cover than in a southern mixed agricultural area. Mortality rate of roe deer as measured by radio-telemetry was high (0.31 in adults and 0.66 in juveniles) during the severe winter compared to the other winters (0.02 for pooled sample). Individual foxes consumed more roe deer (1) during the severe winter than during any other winter, (2) in the northern area than in the southern area during the winter 1976/77, and (3) the more snow-depth increased during 1976/77 (scat and stomach analyses). The ultimate cause of deer death during 1976/77 was most probably malnutrition. 1976/77 was of increasing vole densities and it was not possible to detect any impact of roe deer availability on reproductive success of foxes. If the severe winter had occurred during a vole low, the availability of weakened and dead roe deer would probably have prevented an expected reproductive failure among foxes. Summer mortality of fawns was indirectly attributable to fox predation. Occurrence of roe deer remains in scats of juvenile foxes was inversely related to vole abundance. We suggest that the effect of fox predation on roe deer fawns may be conspicuous in the summer after a severe winter coinciding with a vole low.

[The National Swedish Environment Protection Board, Grimsö Wildlife Research Station, S-770 31 Riddarhyttan, Sweden].

1. INTRODUCTION

The roe deer, *Capreolus capreolus* (Linnaeus, 1758) population in Sweden has increased dramatically during the past century, and after spreading northwards the species is today established in all kinds of habitats over the whole country. The total population is approximately 300,000—400,000 animals. Despite the rapid expansion occasional severe winters have caused heavy mortality for which the prime factor is inanition (e.g. in the winter 1965/66; Borg, 1966, 1970). However, the death rates of roe deer population in Sweden have never been quantified.

The role of the red fox, *Vulpes vulpes* (Linnaeus, 1758) for the winter reduction of the roe deer is a bone of contention. Numerous observations of foxes chasing and killing deer in winter are reported in hunters' literature (e.g. Modigh, 1951, Rosenmüller, 1951; Skuncke, 1951). Borg (1970) found that 13.5% of all roe deer carcasses submitted to the National Veterinary Institute had been killed by fox and other predators. Earlier Borg (1960) noticed that during the winter of 1960 snow structure retarded deer movement and favoured predators. The fox was responsible for nearly 50% of the total number of roe deer killed by predators. However, no information has been gathered on the relative importance of roe deer in the diet of foxes during severe winters, the biomass of roe deer consumed by foxes or to what extent they consume carcasses from inanimate and/or actively killed animals.

Juvenile mortality of roe deer in summer has also been ascribed to predation. Observations of active killing of fawns by foxes are mentioned in the hunters' literature (e.g. Anderson, 1943; Modigh, 1951). Strandgaard (1972) suspected that an increased number of fox litters at Kalø research area in Denmark might have led to higher predation and hence might have had an adverse effect on the survival rate of fawns. This was supported by observations of several remains of roe deer fawns at fox dens. He concluded that foxes are able to kill perfectly healthy fawns. A number of losses of fawns were ascribed to the predation by foxes in the Stammham enclosure in West Germany (Ellenberg, 1978). From stomach content analyses in Switzerland Wandeler (1975) calculated that each fox on average will consume 11 fawns during the period May to July. However, as for winter, no quantifications have been published on the consumption rate of foxes, and the possible impact of fox predation on roe deer population during summer remains an open question.

The reproduction and survival of red fox in middle and northern Sweden are strongly influenced by changes in food supply (Englund, 1970; Lindström, 1982). Thus, the recently increased availability of roe deer might be of great importance for fox reproduction after severe winters.

In this paper we try to throw some light on the relationship between the roe deer and the red fox. Our main objects have been to examine: (1) if red fox predation depresses the density of roe deer populations, (2) if a severe winter with concomitant high mortality of roe deer causes a decline in population density and, (3) if the availability of roe deer during severe winters is high enough to have any effect on the reproductive success of foxes.

We measured the actual death rate of roe deer during winters of

normal snow cover and a severe winter in a specified population as well as we estimated summer mortality of fawns. The proportion of adults actually predated by fox was estimated and mortality rates were compared with consumption of roe deer by fox.

2. STUDY AREA

Roe deer and foxes were studied during 1974 to 1979 within the 14,000 ha Grimsö Research Area in south central Sweden between 59° and 60° N Lat. and 15° and 16° E Long. (Fig. 1). The main part of the research area is rather flat and consists of a somewhat rugged plateau (90–120 meters above sea level), mostly covered by coniferous forest. The habitat is characterized by low ridges, often interspersed by boggy and swampy areas. A more detailed description of the area is given in Cederlund *et al.* (1980). Roe deer were caught and radio equipped in the southern part of the Grimsö Research Area comprising about 1 000 ha ("telemetry area" in Cederlund *et al.* 1979).

Carcasses of foxes were collected from an extended area of approximately 50 km radius around Grimsö, mainly in the county of Örebro (Fig. 1). This area was divided into two regions; (1) northern forested highland in the high boreal region (Ekman, 1922) and (2) flat lowland with many large agricultural areas in the south Scandinavian region (Ekman, 1922). The Grimsö Research Area was considered to be included in region 1. The two regions were divided by the steep geomorphological, climatological and biogeographical gradient, which is referred to as "*limes norrlandicus*" (e.g. Sjörs, 1967).

Weather conditions at Grimsö were representative of inland conditions in south central Sweden. The ground usually was covered with snow from late December to late March. Mean snow depth on February 15 during the period of 1969 to 1979 was 24 cm (Swedish Meteorological and Hydrological Institute).

The winters 1973/74 to 1978/79, except 1976/77, were considered to be moderate or relatively mild with low or normal snow depth (Fig. 2). The winter 1976/77 was extremely snowrich (Fig. 2). For almost two months snow depth exceeded 70 cm. In certain areas it reached 100 to 150 cm. The snow situation was somewhat different in the agricultural low-land (region 2) where the weekly mean snow depth during 1973/74 to 1978/79 (except 1976/77) never exceeded 20 cm (Fig. 2). In 1976/77 snow cover ranged from 50 to 70 cm during January and February.

A major food of foxes in the research area was voles (field vole, *Microtus agrestis* (Linnaeus, 1758), and bank vole, *Clethrionomys glareolus* (Schreber, 1780), (Lindström, 1982). The voles fluctuated in a 4-year cycle (lows 1975 and 1979, high 1977, B. Hörnfeldt, pers. comm.).

3. MATERIALS AND METHODS

Questionnaires were sent annually to hunters in the county of Örebro (Fig. 1), in which they were asked to report whether the populations of roe deer had increased, decreased or remained the same since last hunting season. Some 150

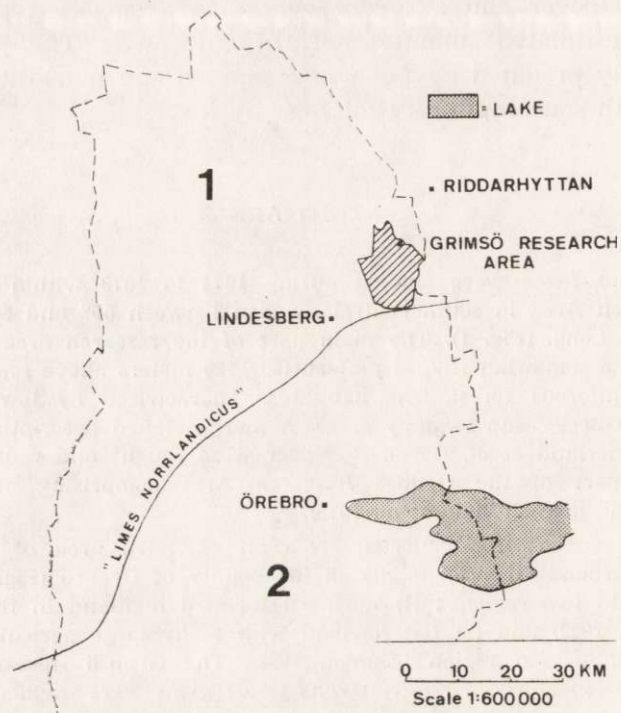


Fig. 1. Map of the situation of Grimsö Research Area and the central and northern part of the county of Örebro.

hunters each year answered the questionnaires in 1974 to 1979. An index ranging between 0 and 2 (Richards & Hine, 1953) was calculated for the change in population size between each successive years.

Data on roe deer survival was obtained by the use of radiotelemetry. Sixty-nine roe deer, caught in box traps, were radiocollared during the period January 1974 to April 1979. Sex, age and weight were noted for each animal. They were tracked for a total of 1432 days. Tracking time varied considerably between individuals due to death, transmitter failure, emigration etc. Ideally, transmitter life lasted for two or three years. Tracking was done intensively from a fixed system during a 24-hour period each week and more extensively by mobile units, at least once a week. Descriptions of field technique and equipment were given by Cederlund *et al.* (1979).

Interval death rate for roe deer was estimated as $1 - [(x-y):x]^n$, where x = tracking days, y = number of dead animals and n = days in interval (Trent & Rongstad, 1974). For this study winter was set to the period from January to March and summer from May to August.

Observations of roe deer carcasses were reported from the entire research area. If possible, sex, age and cause of death were recorded. Tracks in the snow and injuries gave evidence if the fox had consumed or removed parts of the body. Data on reproduction of roe deer were obtained by counting the *corpora lutea* in ovaries from does shot in the Grimsö area. Likewise age structure was assessed

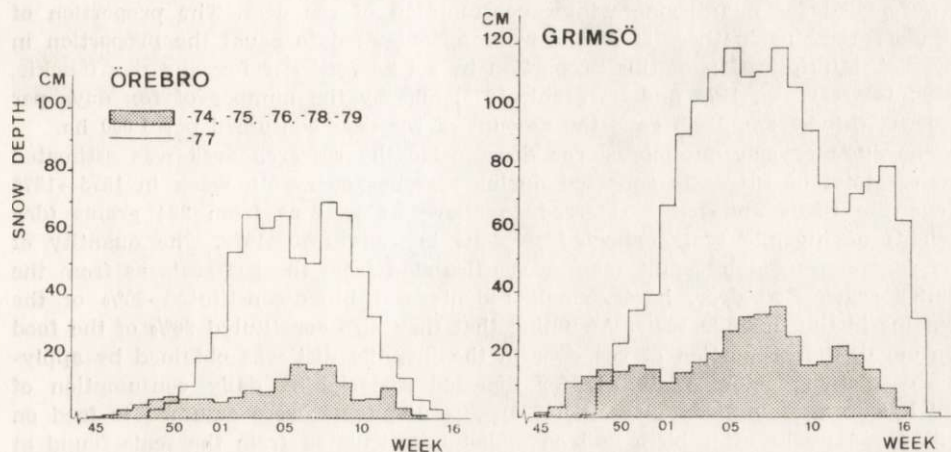


Fig. 2. Snow accumulation in Grimsö Research Area and the city of Örebro from the severe winter 1976/77 and the pooled data from the winters 1973/74, 1974/75, 1975/76, 1977/78 and 1978/79.

from the animals shot within the area. Age was estimated from tooth eruption and wear.

The occurrence of roe deer in the winter diet of foxes inside the research area was measured from 371 scats collected in 1975–1979 after the snow had melted (mid May) along roads and paths, previously cleared from scats in mid November, as well as from 18 scats collected fresh when tracking foxes on the snow in January and February 1977. To calculate the quantity of roe deer consumed the washed and dried weight of roe deer remains per scat was multiplied by (1) a correction factor for weight ingested per dry weight remains in scats (Table 1), (2) number of fox days per 1000 ha (Lindström, 1982) and (3) 7 scats per fox and day (Lockie, 1959; P.O. Palm, pers. comm., and Lindström, unpubl. data).

Furthermore, 911 stomachs from foxes killed during the winters 1976–1979 in regions 1 and 2 were searched for roe deer remains. 306 stomachs from region

Table 1

Correction factors for digested material used in quantification of red fox diet.

Food item	Correction factor used	Base for correction factor
Roe deer	118	Goszczyński, 1974
Mountain hare	41	Mean of correction factors for lagomorphs (Lockie, 1959; Vogtsberger & Barret 1973 ¹ Goszczyński, 1974 and Litvaitis & Mautz, 1976 ¹)
Small rodents	23	Lockie, 1959 and Goszczyński, 1974
Birds	57	Lockie, 1959 ²

¹ Recalculated correction factor from bioenergetic data assuming 50% loss of undigested material when washing the scat (Lindström, unpubl. data).

² 61 for large birds and 45 for small birds. Ratio between large and small birds in droppings being 2:1.

l were used for quantifying winter consumption of roe deer. The proportion of roe deer remains in these stomachs was approximated to equal the proportion in the diet. Multiplication of this proportion by 0.4 kg food per fox and day (Lockie, 1959; Goszczyński, 1974 and Sargeant, 1978) and by the number of fox days per 1 000 ha (Lindström, 1982) gave the amount of roe deer consumed per 1 000 ha.

The summer consumption of roe deer inside the research area was estimated from a total of 504 scats collected during searches every 4th week in 1975—1978 along the roads and paths referred to above as well as from 294 grams (dry weight) of juvenile scats collected at dens in June 1975—1979. The quantity of roe deer consumed by adult foxes was calculated from the 504 scats as from the winter scats. Roe deer, hares, small rodents and birds constituted 90% of the remains in the juvenile scats. Assuming that they also constituted 90% of the food consumed, the proportion of roe deer in the juvenile diet was obtained by applying correction factors (Table 1) for digested material. A daily consumption of 0.24 kg/cub was applied (Sargeant, 1978). Juvenile foxes were assumed to feed on milk for 4 weeks after birth and on a diet as calculated from the scats found at dens for 7 weeks. For late summer the diet was derived from scats found on the roads and paths and a defecation rate of 7 scats per day was used as a base for calculations also for juveniles.

4. RESULTS AND DISCUSSIONS

4.1. Roe Deer Population

According to the questionnaires, a continuous increase in deer numbers, interrupted by the hard winter of 1976/1977, took place in the whole county of Örebro (Fig. 3). The difference between the distribution of answers over the three alternatives in 1977/78 as compared to the other winters was significant at $P < 0.001$. In the northern forested region (1) the population showed a steeper increase and this was also more drastically interrupted by the hard winter than in the southern agricultural region (2). It should be noted that this method does not discriminate between reproducing and other animals. Thus, the decline after 1976/77 might only have affected surplus individuals.

Track counts on snow within the "telemetry area" in March and April 1976 indicated a mean density of about 35 individuals/1000 ha (Cederlund, unpubl.). The roe deer population was considered to increase when the surveys were initiated but in 1976 the population had stabilized at the social carrying capacity of the area (cf. Strandgaard, 1972 and Bobek, 1977), a view supported by the fact that marked young deer every year emigrated from the area. Emigration also occurred in the spring following the winter 1976/77, although more animals than usual remained in their natal areas (Cederlund, unpubl. data). Therefore, we believe that the density of reproducing roe deer was not greatly affected by the severe winter.

Due to a very low hunting pressure the mean age of resident animals was unusually high prior to the winter 1976/77, which may have made them more susceptible to severe winter conditions.

4.2. Winter Losses

Losses of radio equipped roe deer were frequent in the severe winter 1977 when 7 animals died out of 26 (Table 2). Only one radio equipped

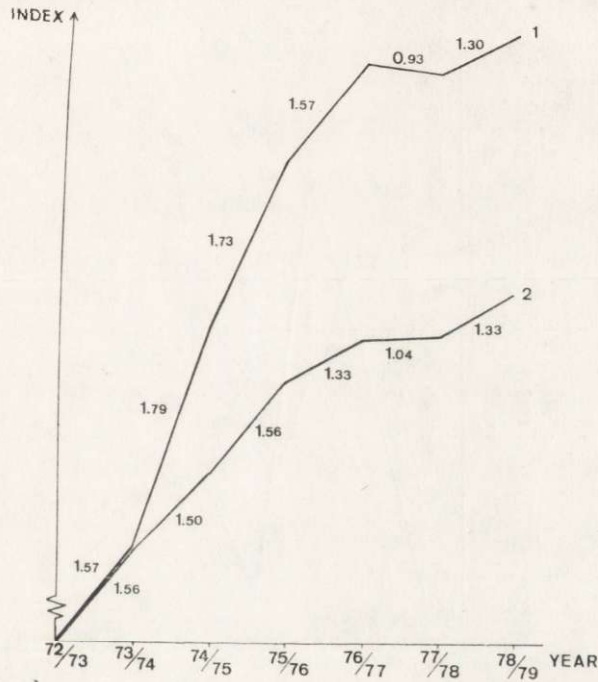


Fig. 3. Relative changes in the roe deer populations in areas 1 and 2 (Fig. 1) according to yearly questionnaires. The slope of the line is proportional to mean answer; 2 = vertical up, all answers: increase; 0 = vertical down, all answers: decrease; 1 = horizontal, mean answer: no change. Mean answer is indicated along the line.

animal died in all the other winters. Hence the interval death rate was higher in 1977, amounting to 0.31 for adults and 0.66 for juveniles than in the pooled material of the other winters (mean death rate = 0.02). Data from captures during winters 1973—1978 revealed an adult/juvenile ratio of 60 : 40. Assuming that the autumn population was 35 individuals/1000 ha the actual number in the two age classes would be 21 adults and 14 juveniles/1000 ha. In the winter 1976/77 22 reliable observations of dead deer were reported from the research area. Observations of

carcasses during the other winters were scarce, usually one or two per season.

From capture and harvest data it was evident that the high loss during the winter 1976/77 did not significantly affect the sex ratio and proportion between resident yearlings and adults as compared to the other years. Thus, the number of juveniles to establish home ranges in their natal area was enough but there might also have been a recruitment of young animals through immigration from southerly areas with lower winter losses.

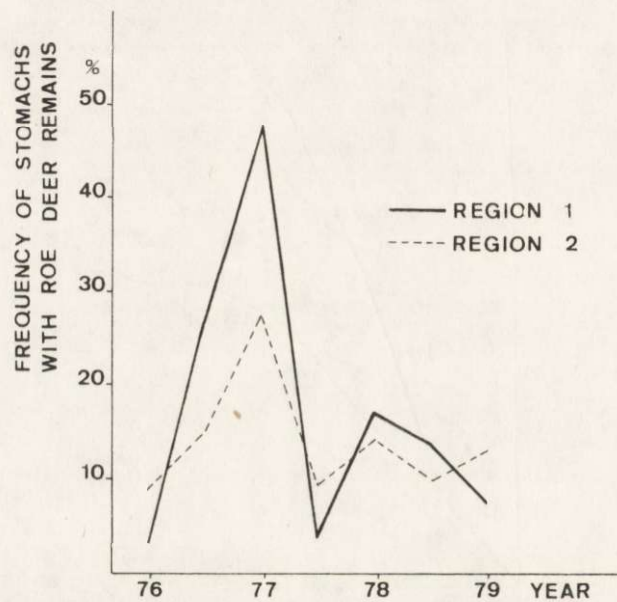


Fig. 4. Frequency of fox stomachs with roe deer remains in early winter (Oct. to Dec.) and late winter (Jan. to March) 1976–1979 from the two regions. Total sample = 911. Single samples ranging from 32 to 106.

The high roe deer mortality during the winter 1976/77 was accompanied by an increase of roe deer in the diet of foxes (Fig. 4, $P < 0.001$ in χ^2 -test of frequency of stomachs with roe deer remains during the first three months of 1977 as compared to the other years). Furthermore, during the winter 1976/77, the frequency of occurrence of roe deer remains was higher in the stomachs from the forested region (1) than in those from the agricultural region (2) (48% vs 27% $P < 0.05$, χ^2 -test, Fig. 4) corresponding to the difference in snow cover (Fig. 2) and in the change of the roe deer populations according to the questionnaires (Fig. 3). A similar relationship between snow and roe deer in the diet of foxes was also evident within the winter; The percent weight of roe deer

Table 2

Interval death rate of radio equipped roe deer in Grimsö Research Area. Winter is defined as the period January to March, summer as May to August. Figures in parenthesis indicate total number of radio equipped roe deer.

Item	Total No. tracking days	Number of dead roe deer			Interval death rate	No. of dead roe deer/1000 ha
		juv.	ad. M	ad. F		
Winter 73/74—78/79 (except 76/77)	6255	0 (22)	1 (18)	0 (16)	0.02	0.7
Winter 76/77						
Adults	1314	—	4 (9)	0 (10)	0.31	6.5
Juveniles	333	3 (7)	—	—	0.66	9.2
Summer season 74—79	6440	a	2 (31)	1 (26)	0.05	1.0—1.5

a—No juveniles were radio equipped.

remains in the stomach contents from foxes killed in the forested region (1) was positively correlated with the increase of snow cover throughout the winter ($r=0.84$, $0.05 > P > 0.01$, one-tailed test, Fig. 5).

As the quantification of the consumption by foxes is hampered by many uncertainties, we have chosen to present different calculations and discuss possible sources of bias.

The estimated amount of roe deer consumed per 1000 ha during January—March in ordinary winters varied between 1 and 39 kg with a mean of 9 kg for the stomach analyses and 27 kg for the scat analyses (Table 3). No scats were collected when tracking foxes on the snow these winters. During 1977, estimates of 30, 68 and 529 kg roe deer consumed were obtained from stomachs, mid-May scats and mid-winter scats respectively (Table 3). The figures are to be compared with the

Table 3

Consumption (kg)/1000 ha of roe deer by foxes, during the period January through March (week 1—13) normal winters (1974/75, 1975/76, 1977/78 and 1978/79) and the severe winter 1976/77 as compared to estimated amount of roe deer dying during the same period. Figures in the parentheses indicate number of stomachs and scats analysed.

	No. of fox days	Roe deer consumed kg			Roe deer dying kg ¹
		stomachs	scats collected in May	midwinter scats	
Mean of normal winters	405	8 (249)	27 (268)	—	16
1977	381	30 (57)	68 (103)	529 (18)	289

¹ Mean live weight of roe deer as in Table 5. Number of roe deer as in Table 2.

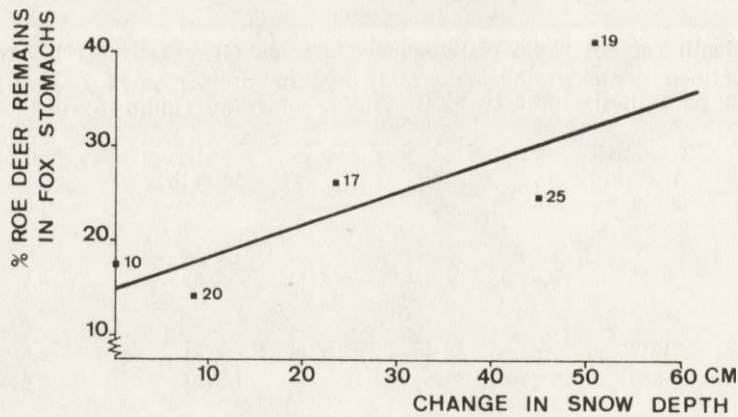


Fig. 5. Percent of roe deer remains (weight) in the contents of fox stomachs from region 1 during 1976/77 in relation to increase in snow depth every 4th week. Number of stomachs are indicated along with each point.

estimates of 16 kg roe deer dying during January—March in ordinary winters and 289 kg dying during 1977.

The calculations based on stomachs and mid-May scats in 1977 probably underestimated roe deer occurrence. Stomachs were mainly obtained from foxes shot at bait and in baited traps (Lindström, *in press*) and thus the contents were biased towards the material used for bait (chicken, fish etc.). The roads and paths used for scat collection in May 1977 had probably been utilized by fox mostly in the early and late winter as the deep snow cover during mid-winter had made the forest floor equally difficult to traverse everywhere. Normally the foxes probably preferred the roads and paths.

Thus, the scats from May 1977 were likely to have been biased towards periods of relatively low roe deer mortality. On the other hand, the material of scats collected when tracking foxes on the snow was likely to have been biased in the opposite direction as good tracking conditions and severe conditions for roe deer coincided.

From a material of occasional trackings and observations in the sur-

Table 4

The consumption activity of fox on roe deer carcasses in Grimsö Research Area the winter 1976/77.

	Parts of carcass removed by fox	No carcass removed by fox	Total
Found < 1 week after death	4 ¹	4	8
Found > 1 week after death	9	—	9

¹ 3 known to have been killed by fox.

roundings of Grimsö, we know at least 4 cases of red fox killing healthy roe deer (health determined from subcutaneous and coronary fat; Borg, 1970). Signs in snow made it obvious that the fox had taken advantage of snow conditions in particularly favourable terrain (weakened or injured deer were observed being attacked in the open). From hunters we have reliable information on instances of two foxes hunting the same deer. Also, in one case, our own observations indicated two foxes participating in the attack. However, of five radio equipped deer found within a week after death, only one was injured by fox. Four were complete without visible injuries and no tracks from foxes in the snow in the surroundings. They were considered as strongly emaciated with almost no visible subcutaneous and coronary fat and gelatinous bone marrow. Table 4 presents the fate of radio equipped and unmarked roe deer carcasses within the entire research area. This combined material comprises another three animals (not radio-collared) found injured by fox within a week after death. All carcasses found more than a week

Table 5

Live weight (kg) of roe deer during the severe winter 1976/77 (S) and the winters 1973/74 to 1975/76 (M). Weights are recorded during the period 1 January to 31 March.

	Juveniles		Adults			
	M	S	M, ♂	S, ♂	M, ♀	S, ♀
Mean value	17.9	14.9	27.5	24.3	25.8	22.4
SE	0.6	0.3	0.8	0.9	0.6	0.6
Range	16.1—22.0	13.5—15.7	21.2—30.8	21.0—28.0	20.0—27.6	19.0—25.8
n	9	8	8	8	12	12

after death had been visited by foxes. Despite the small material our data support findings by Borg (1970) that the actual cause of death among roe deer during severe winters emanate from other factors than fox predation.

The mean live weight of roe deer amounted 10 to 16% less in the winter 1976/77 as compared to the other winters (Table 5). The difference was significant for both adult sexes as well as for juveniles (*t*-test, $P < 0.05$). The measured juvenile weights did not even overlap. Cederlund *et al.* (1980) showed that the roe deer fed almost exclusively on twigs etc. during the winter 1976/77 while their normal winter diet to a large extent consisted of material from the field layer. We conclude that the probable proximate and certainly the ultimate cause of most of mortality of roe deer during 1976/77 was inanition due to the problems of obtaining food of high nutritional value and due to the high energetic expenditures of any activity in the deep snow (see Moen, 1973). Even

when foxes actually killed the animals, it must often have been emaciated and thus doomed individuals.

The reproductive success of foxes, as measured by counts of active dens inside the Grimsö Research Area, was at bottom in years of low vole abundance due to food shortage during late winter and spring (Lindström, 1980 and 1982). During years of increasing or high vole densities a constant number of active dens were found. The hard winter 1976/77 occurred during the increase phase of the vole cycle.

No effect of the abundance of emaciated roe deer on fox reproduction could be detected. However, if it had occurred during a vole low, the extra food available in the shape of roe deer might have been enough to prevent a reproductive failure among the foxes. The 289 kg roe deer dying per 1000 ha during January to March would have been enough to fulfill the nutritional requirements of 8 foxes during the same period. The spring population of foxes never exceeded 5 individuals per 1000 ha (Lindström, 1982).

Table 6

Estimated amount of roe deer consumed by red fox per 1000 ha during summer May—August. Means of 4 years (1975—1979).

Period	Cohort (foxes)	Mean No. of fox days	No. of scats analyzed	Grams of scats analyzed	Mean biomass of roe deer consumed (kg)
Spring, early summer (week 0-28)	adults	177	214		18
	juveniles	160		294	13
Late summer (week 28-36)	ad+juv	409	290		18
Total period					49

It is somewhat puzzling that foxes did not utilize roe deer for food more during vole lows. Obviously they have an innate capability of learning to hunt deer and perhaps also to hunt cooperatively (see above). A probable cause of this inconsistency may be that foxes mature before their first winter. Dispersal of most young (especially males) occurs in late autumn (Storm *et al.*, 1976) and there is little chance of parents teaching these to hunt adult deer, which requires snow cover.

However, some young (females) remain within their natal territories to form family groups together with their parents (Macdonald, 1977; Lindström, 1982) but perhaps the ties between members of such groups are too loose to permit learning extensive cooperative hunting. The mean life expectancy of subadult foxes (1.5 years, Lindström, in press) may also be too short for a large proportion of the foxes to gain the necessary experience on their own or for a tradition to become established.

4.3. Summer

Summer mortality was low among adult roe deer. Only three radio equipped animals were found dead during the period 1 May to 31 August yielding an interval death rate of 0.05. The actual cause of death was unknown in all cases. Considering that the adult population in summer was approximated to 20 to 30 roe deer/1000 ha (Cederlund, unpubl. data) the loss would be 1.0 to 1.5 animals (see Table 2).

Summer mortality among juveniles could only be estimated indirectly. Analysis of ovaries revealed that on average 2.20 *corpora lutea* were produced per adult female ($n=23$). Assuming a general ovum loss of about 10% (Markgren, 1969 and Borg, 1970) one obtains a birth rate of 1.98 fawns per doe. Captures from all winters except 1976/77 indicated 1.06 fawns/doe. Accounting for yearling does, which constituted about 21% of the adult female population (calculated from the harvested population within the research area) the winter ratio would be 1.33/mature doe. This, death rate from birth in early June to trapping season in winter would be 34% or 7 fawns per 1000 ha (10 pregnant females/1000 ha and assuming no doe mortality, Cederlund, unpubl. data).

Table 7
Percent roe deer and small rodents (mainly voles) in the diet of juvenile foxes different years.

Year	% Roe deer	% Small rodents	Grams scats analyzed	Vole index ¹	
				<i>Microtus</i>	<i>Clethrionomys</i>
1976	46	3.3	93	0.10	3.29
1977	23	47	53	3.16	5.20
1978	26	33	69	0.21	3.38
1979	47	9.3	79	0.21	1.16

¹ Data from B. Hörnfeldt (pers. comm.)

Calculations of the consumption of roe deer by foxes during summer yielded a mean annual figure of 49 per 1000 ha (23 to 97 kg, Table 6), 31.1 kg of these having been consumed before early July. The proportion of fawns is unknown.

Assuming a mean fawn weight of 3 kg before July and 8 kg during July—August (Stubbe, 1966; Wandeler & Huber, 1969; Berggren, 1974) the 49 kg consumed roe deer makes 5—10 fawns plus the one adult estimated via radio tracking (above). Thus, most of the summer mortality of fawns may be attributable to red fox predation (if the foxes had killed all fawns they consumed).

There was a non-significant tendency of a lower recruitment of young into the winter population of roe deer during 1977/78 as compared to the years before 1976/77 (0.77 fawns per adult doe among captured

animals (9 does) 1977/78 vs 1.05 (34 does) the other years). Ellenberg (1978) found that the mortality of roe deer fawns was inversely correlated to the weight of their does. The mortality of Australian lambs could also largely be attributed to the quality of the ewe and the lamb (see Lloyd 1980 for a review). The frequency of roe deer remains in scats from adult foxes during early summer 1977 was very high (31 vs 9—17% other years, Lindström unpubl.). However, no such increase was noted among scats from juvenile foxes at dens. Frequency of roe deer in the diet of juveniles was inversely correlated to frequency of small rodents, which in turn reflected the vole cycle (Table 7).

Summing up, the increased roe deer mortality during the severe winter 1976/77 probably reduced at least the non-reproductive cohort of the population next season. Although raised consumption of deer by red fox was shown to accompany the high deer mortality, and although the biomass consumed formed a large proportion of the loss, fox predation was probably not the main factor responsible for the mortality. Rather, the snow *per se*, which covered the nutritionally important food of the field layer and forced the deer to browse on twigs etc., induced malnutrition which in turn weakened and killed many deer. Even though the severe winter was the ultimate factor causing high roe deer mortality some animals might have survived if there had been no fox predation. However, this number was not possible to calculate.

Young fawns are a more suitable prey for foxes and the summer mortality of these was indirectly attributable to fox predation. In this study, the density of reproducing deer did not seem to be heavily influenced neither by severe winter mortality nor by ordinary summer mortality. However, the hard winter took place during the increase phase of the vole cycle and foxes therefore had plenty of voles to eat. If it had occurred during a vole low, the foxes perhaps had devoted more time to hunting weakened deer. Presumably the additional food provided by dead or weakened deer would have been enough to prevent the reproductive failure among foxes, which otherwise will accompany a vole low. As consumption of roe deer by juvenile foxes was shown to be negatively correlated with consumption of small rodents and thus with the 4-year vole cycle, the pressure on deer fawns presumably will be very high if a vole low and a severe winter coincide. This effect may be further reinforced by the poor condition of does and their newborn fawns after a hard winter. Assuming that a hard winter occurs every 10th year, such a coincidence would occur 2.5 times every century. In such a situation the effect of fox predation on a local roe deer population may be considerable.

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Göran CEDERLUND i Erik LINDSTRÖM

WPŁYW SUROWEJ ZIMY I DRAPIEŹNICTWA LISÓW
NA ŚMIERTELNOŚĆ SARN

Streszczenie

Badania prowadzono na 14 000 ha Stacji Badawczej Grimsö w południowo-centralnej Szwecji (Ryc. 1). Autorzy postawili sobie za cel stwierdzenie: (1) czy drapieżnictwo lisów ma wpływ na obniżenie populacji sarn; (2) czy surowa zima z towarzyszącą jej wysoką śmiertelnością sarn powoduje spadek zagęszczenia populacji i (3) czy dostępność sarn w ciągu surowej zimy jest wystarczająco duża aby zapewnić zwiększony rozród lisów. Na podstawie odpowiedzi w kwestionariuszach, wypełnianych co roku przez 150 myśliwych, określono że populacja sarn w okresie badań, ma tendencję wzrostową z wyjątkiem przerwy w czasie surowej zimy 1976/77. Przerwa ta była bardziej wyraźna w północnych, zalesionych terenach z głębszą okrywą śnieżną niż w południowych terenach rolniczych (Ryc. 2, 3). Poziom śmiertelności sarn oznaczony przy użyciu radio-telemetrii był wyższy (0,31 u dorosłych i 0,66 u młodych) w ciągu tej surowej zimy w porównaniu z in-

nymi zimami (0,02 łącznie dla obu grup) (Tabela 2). Na podstawie analiz treści żołądkowej 911 lisów i analiz kału z 371 prób stwierdzono (Tabela 1), że: pojedynczy lis zjada więcej sarn: (1) w ciągu surowej zimy niż w ciągu innych zim, (2) na terenach północnych niż na południu w ciągu zimy 1976/77 i (3) tam gdzie grubość okrywy śnieżnej wzrasta w ciągu zimy 1976/77 (Ryc. 4, 5; Tabele 3, 4). Podstawową przyczyną śmierci sarn w zimie 1976/77 było niedożywienie (Tabela 5). W ciągu roku 1976 wzrastało zagęszczenie norników i nie dało się w związku z tym wykryć dodatniego wpływu dostępności sarn na sukces rozrodczy lisów. Jeżeli surowa zima wystąpiłaby w ciągu niskiego stanu liczebności norników, dostępność osłabionych i padłych sarn zapobiegłaby prawdopodobnie przypuszczalnemu zmniejszeniu rozrodu lisów. Letnia śmiertelność kozłat była pośrednio przypisywana lisom (Tabela 6). Występowanie resztek sarn w kale młodych lisów było odwrotnie zależne od obfitości norników (Tabela 7). Autorzy sugerują, że wpływ drapieżnictwa lisów na kozłata jest bardziej widoczny w lecie następującym po ciężkiej zimie, pokrywanej się z niską liczebnością norników.