Wolf Canis lupus predation on moose Alces alces and roe deer Capreolus capreolus in south-central Scandinavia

Authors: Olsson, Olof, Wirtberg, Jan, Andersson, Marianne, and Wirtberg, Ingrid

Source: Wildlife Biology, 3(1) : 13-25

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.1997.003

Wolf *Canis lupus* predation on moose *Alces alces* and roe deer *Capreolus capreolus* in south-central Scandinavia

Olof Olsson, Jan Wirtberg, Marianne Andersson & Ingrid Wirtberg

Olsson, O., Wirtberg, J., Andersson M. & Wirtberg I. 1997: Wolf *Canis lupus* predation on moose *Alces alces* and roe deer *Capreolus capreolus* in south-central Scandinavia. - Wildl. Biol. 3: 13-25.

During 1988-1992, 684 scats were collected throughout the year in the territory of the only reproducing family group (mean five individuals) of wolves *Canis lupus* in Scandinavia. Moose *Alces alces*, roe deer *Capreolus capreolus*, and badger *Meles meles* constituted the three most important prey species, and hair from them was found in 52%, 50%, and 19% of scats, respectively. When compensating for different area/volume ratios in prey species of different size, these three species were estimated to constitute 97% of the biomass ingested. The proportions of moose, roe deer, and badger were 66%, 27%, and 8% by mass, and 25%, 52%, and 23% by number, respectively. Young-of-the-year dominated two samples of dead moose (51% of 65 killed by wolves; 43% of 155 killed by hunters), but no significant differences between the samples were found in any age class. Wolves killed significantly more female moose (76%) than hunters (53%), and among wolf-predated moose, no male was older than two years. Mean winter density of moose and roe deer in the wolf territory (523 km^2), estimated by fecal pellet group counts, was 1.5 moose and 0.4 roe deer/km^2. Moose density decreased slightly at the end of the study, but it was estimated that wolves killed only about 5% of the moose population each year and that this could be compensated for by a decrease of about 10-20% in the hunter kill. In spite of a high predation pressure from wolves, in addition to predation from an increasing lynx *Lynx lynx* population, the density of roe deer increased threefold. It is concluded that the future predation pressure on moose may be more pronounced if the density of wolves increases, and roe deer may be more affected by predation when the present favourable ecological conditions cease.

Key words: badger, Canis lupus, prey, scat analysis, ungulate, wolf

Olof Olsson, Department of Zoology, Villavägen 9, Uppsala University, S-752 36 Uppsala, Sweden and Department of Zoology, Stockholm University, S-106 91 Stockholm, Sweden
Jan Wirtberg & Ingrid Wirtberg, Bergsidan 8, S-685 97 Östmark, Sweden
Marianne Andersson, Department of Zoology, Lund University, S-223 62 Lund, Sweden

Received 16 October 1996, accepted 13 February 1997

Associate Editor: Jon E. Swenson

The pattern of predation by wolves *Canis lupus* has been examined in a large number of studies, and ungulates constitute the main natural prey of the wolf almost throughout its entire world range (e.g. Mech 1966, Kuyt 1972, Peterson 1977, Fuller & Keith 1980, Carbyn 1983, Ballard, Whitman & Gardner

1987, Salvador & Abad 1987, Jedrzejewski, Jedrzejewska, Okarma & Ruprecht 1992, Jhala 1993, Smietana & Klimek 1993, Meriggi, Brangi, Matteucci & Sacchi 1996). Hence, ungulates are also important prey for wolves in Europe (see Okarma 1995 for review). An important and debated question is the effect of wolf predation on ungulate populations (e.g. Pimlott 1967, Bergerud, Wyett & Snider 1983, Messier & Crête 1985, Messier 1991, Jedrzejewski et al. 1992, Dale, Adams & Bowyer 1994, Messier 1994, Okarma, Jedrzejewska, Jedrzejewski, Krasinski & Milkowski 1995), and the potential competitive conflict with hunters for ungulates in some regions (e.g. Gasaway, Stephenson, Davis, Shepherd & Burris 1983, Boyd, Ream, Pletscher & Fairchild 1994).

On the Scandinavian Peninsula (Norway and Sweden) wolves were widely distributed and relatively common until about 100 years ago, but the species became almost eradicated due to human persecution (Arnesson-Westerdahl 1987, Bjärvall 1988). Even though the species was protected in 1966 in Sweden, and in 1973 in Norway, only a few individuals seemed to occur in the northernmost parts of the peninsula. Only one instance of reproduction was reported in the 1960s and one in the 1970s. The latter, which took place in 1978 in Vittangi, in the Swedish province of Norrbotten, was the last known reproduction in northern Sweden (Bjärvall 1988). However, in the early 1980s wolves appeared in the south-central part of Scandinavia, mainly in the provinces of Värmland and Kopparberg in Sweden, and Hedmark in Norway. The first confirmed breeding in these areas took place in northern Värmland in 1983, almost 1,000 km south of the previous known breeding site in Norrbotten. Breeding then occurred annually in one specific area in Värmland during the subsequent decade by at least two succeeding alpha pairs (pers. obs.). Our five-year study deals with these wolves, which at the time was the only reproducing pair in Scandinavia, and probably the smallest wolf population in the world.

After the termination of our study there has been a small increase in the number of wolves in Sweden and a few more territories have become occupied. So far these few events of reproduction, except one, have taken place outside the principal areas for both livestock (mainly in southern Sweden and parts of Norway where keeping of free ranging sheep *Ovis aries* is extensive) and reindeer husbandry (central and northern mountain regions) in Scandinavia. This region, which mainly consists of coniferous forests (the 'taiga'), is probably also the area most suitable for a potential future increase in the wolf population in Scandinavia. The predominant potential conflicts with humans in this region are connected with hunting; i.e. predation on moose *Alces alces* and roe deer *Capreolus capreolus*, but also with the fact that wolves sometimes kill pet and hunting dogs (dogs are normally used in most types of hunting in Scandinavia, and some of them are worth more than USD 5,000). The killing of sheep by wolves is another existing potential conflict.

The major aim of this study was to investigate the pattern of wolf predation and to evaluate the impact of wolves on moose and roe deer populations in a region suitable for increases in wolf numbers. Data on three different aspects were collected by parallel investigations of: 1) wolf diet by scat analysis, 2) sex and age of moose killed by wolves and hunters, and 3) ungulate census in the wolf territory by fecal pellet group counts. Such data are important for the future management of wolf, which probably is the most endangered native mammal species in Scandinavia.

Methods

Study area and the wolf pack

The wolf territory of this study was situated at the border between Sweden and Norway, and the wolves spent almost all their time on the Swedish side in the province of Värmland (position of territory core area: 60°30'N, 12°50'E), in south-central Scandinavia. We estimated the territory to hold a mean number of five individuals during the study. The pack size varied from two to five individuals. In addition, more or less throughout the whole study period, there were one or a few loners in the area which seemed loosely connected to the pack. As we dealt with the only existing family group of wolves on the Scandinavian Peninsula at the time, consequently no neighbouring territories existed. We cannot rule out the possibility that we were actually dealing with two subsequent alpha pairs within the same area. Reproduction took place each year, which we verified by visual observations, presence of cub hair in scats (see below), and tracks on the first snow in autumn. Litter sizes were unknown, but during the entire study period we never recorded more than two cubs to be alive in the autumn. Territory size during winter was approximately 600 km^2, determined from snow tracking, and

it had more or less the same distribution throughout the whole study period.

The study area is hilly with altitudes ranging from 120 to 600 m a.s.l., and mainly covered with boreal forests of Norway spruce *Picea abies* and Scots pine *Pinus sylvestris*. Deciduous trees, e.g. birch *Betula spp.*, aspen *Populus tremula*, alder *Alnus incana*, and willow *Salix spp.*, occur mainly at rivers, lakes, human settlements, and as primary vegetation in the numerous clear cuttings. Logging activities are extensive and forest gravel roads penetrate the entire landscape.

Most precipitation falls during summer and temperatures range between 10° and 20°C. During winter, temperature normally ranges between 0° and -25°C, and the snow cover often exceeds one metre. However, throughout this study winters were unusually mild, the snow depth was much below normal and varied little between years. Only in the winter of 1990/91 did the depth exceed 0.5 m from mid-January to mid-March (snow depth was measured weekly at one mid-altitude spot in the territory throughout the study). However, the snow cover varied considerably with altitude within the territory.

Roe deer have undergone a dramatic population increase in Scandinavia during the last decades, and have relatively recently spread to the study area (Liberg, Cederlund & Kjellander in press). Here they live more or less on the edge of their possible range, restricted by deep snow and partly dependent on artificial feeding. The moose population peaked in the late 1970s and early 1980s, and thereafter stabilised at a somewhat lower density (Cederlund & Markgren 1987, Hörnberg 1995). The moose population is strongly influenced by human hunting, and the annual harvest is often between 1/3 and 1/2 of the total population.

The population of lynx *Lynx lynx*, which mainly feeds on roe deer and therefore is a potential competitor for the wolf, has increased relative to the increase in roe deer (Liberg & Glöersen 1995). Red fox *Vulpes vulpes*, an important predator on roe deer fawns (Linnell, Aanes & Andersen 1995), was almost totally absent during the study period due to sarcoptic mange (Lindström, Andrén, Angelstam, Cederlund, Hörnfeldt, Söderberg, Lemnell, Martinsson, Sköld & Swenson 1994). Brown bear *Ursus arctos* occurs only sporadically in the study area.

Diet investigation by scat analysis

Unlike many other studies only using kills observed in the snow for analyses of winter diet (e.g. Peterson 1977), we chose to investigate wolf diet by scat analysis all year round, and hence we avoided methodological differences between summer and winter. By regularly patrolling forest gravel roads by car, we collected 684 wolf scats from March 1988 through June 1992. After rinsing and drying the scats, hair from prey species were identified by microscopic examination of (i) impression of scale structure, and (ii) cellular structure in cross sections; the latter being the only way of distinguishing moose hair from roe deer hair. Several tufts of hair were examined from each scat, and if macroscopic examination suggested presence of more than one type of hair, additional samples were examined. Comparisons were made to reference collections (Lund University) and the literature (Wildman 1954, Appleyard 1960, Brunner & Coman 1974, Debrot, Fivaz, Mermod & Weber 1982, Blazej 1989, Teerink 1991). Several blind tests were made, especially to establish reliability in distinguishing between moose and roe deer (several parts of the body of both juvenile and adult individuals of both species were checked) and no errors were detected.

In autumn, moose calves and roe deer fawns moult their reddish juvenile fur to grey/brownish fur similar to that of adults, and therefore these two types of hair are the only age categories distinguishable when analysing scats. Consequently, in winter, hair classified as coming from 'adult' moose or roe deer (see e.g. Table 1), still may come from young-of-the-year.

As prey species differ in volume/surface ratio, large species leave less hair in wolf scats per unit mass consumed than small species (Mech 1970). Consequently, by only using frequency of occurrence of hair in scats as an estimate of species composition in the diet, large prey species will be overestimated by number and underestimated by mass. Therefore, we corrected the data using a linear regression equation ($Y = 0.439 + 0.008X$) between prey mass of each species per scat and the total mass of an average-sized individual of each prey species (Weaver 1993, see also Floyd, Mech & Jordan 1978). The estimated mean masses of the different prey species, X in the equation were the following (the numbers in parenthesis represent the mean mass estimated to have been utilised by wolves, subsequently used for back-calculation for proportion by number of consumed prey): moose with adult fur 200 (100) kg, adjusted for predominance of females and young, see below; moose with juvenile fur taken before 15 July 30 (25) kg; moose

with juvenile fur taken after 15 July 70 (50) kg; roe deer with adult fur 25 (17) kg; roe deer with juvenile fur taken before 15 July 7 (5) kg; roe deer with juvenile fur taken after 15 July 12 (10) kg; badger *Meles meles* 12 (9) kg; beaver *Castor fiber* 15 (12) kg; hare *Lepus timidus* 3.2 (3) kg; bird *Aves* 1.0 (1.0) kg; domestic sheep 30 (20) kg. Voles and lemmings *Arvicolinae* were not adjusted because their low mass is outside the range on which Weaver's (1993) regression equation was based; instead they were assumed to have been consumed in one piece and their mass was estimated to be 25 grams.

One must bear in mind that the scat analysis method has its limits in correctly reflecting the importance of different prey species (see Ciucci, Boitani, Pelliccioni, Rocco & Guy 1996). For example, the size and sex of the individual prey is not determined and one has to estimate the mass of the consumed prey. Moreover, although Weaver's (1993) equation covered the size range of the prey animals of this study (except voles and lemmings), it was partly based on other prey species. Two important species in this study, roe deer and badger, were not included in the feeding experiments leading to the equation.

Sex and age of moose killed by wolves vs hunters

During 1985-1992, we found 65 moose carcasses, the majority during winter, that were defined as having been killed by wolves. We often examined carcasses several days, or even weeks, after killing in order not to disturb the wolves. Consequently, it was sometimes difficult to determine the cause of death, but we only included kills where tracks and/or injuries suggested that the moose had been killed by wolves. The lower jaw was collected for age determination, which we made by counting annual cementum layers of the first molar (M1) (Markgren 1969). Sex was determined by presence or absence of antlers (or rudiments).

For comparison we also investigated age and sex in a sample of moose killed by hunters. This sample contained all moose (N = 155) shot in hunting areas owned by 'Stora Skog AB' within parts of the wolf territory during two years, 1989 and 1991. In general there were no restrictions on the age and sex classes which could be killed, but hunters were generally recommended to take calves and to avoid shooting large bulls, which are very rare. Hunters generally also tended to avoid shooting cows with calves and to prefer males. Hence, there may have been a significant surplus of females in the population.

Ungulate census

During the first winter, 1987/88, we found tracks of the alpha pair over an area of 523 km^2 on the Swedish side of the border, the area approximately corresponding to the wolf territory. In this area we made an annual ungulate census each spring (1988-1992) by fecal pellet group counts (see Neff 1968) in 60 permanent squares of 1 km^2. Of these, 25 and 35 squares were randomly distributed above and below the median altitude (390 m a.s.l.), respectively. The sampling frequency at lower altitudes was higher because of an expected higher density of ungulates there in winter. In each of these squares we walked along two parallel transects, 500 m apart, and every 50 m we counted pellet groups in circular spots with the size of 25 m^2 for moose and 10 m^2 for roe deer. The spot size for the roe deer census was smaller in order to minimise the risk of overlooking the smaller-sized pellet groups (Smith 1968).

To estimate the mean density, N, of moose and roe deer during each winter we used the formula

$$N = \frac{D/A}{T \times F}$$

where D is the number of pellet groups found, A the total area sampled, T the number of days during which the pellets accumulated (from defoliation to time for pellet groups counts which were made immediately after snow melting; 247 and 229 days above and below median altitude, respectively), and F the average number of defecations per day and individual; 14 for moose (K. Wallin, pers. comm.); and 21 for roe deer (modified from Mitchell, Rowe, Ratcliffe & Hinge (1985) and O. Liberg, pers. comm.).

However, these estimates of ungulate densities do not give relevant measures of variance and therefore, variance is not presented in Figure 4. For statistical analysis of differences between years, more reliable results are achieved by comparing mean number of pellet groups in winter, which indirectly indicates ungulate density. This was done using the likelihood ratio test, according to method and statistical software (PELANAL) described and provided by White & Eberhardt (1980). To do this we first used the goodness of fit test to determine whether our pellet group data fitted the negative binomial distribution. For moose, we pooled the number of pellet groups found in the 20 spots in each transect and used each transect as a unit (resulting in N = 120, 500 m^2 each).

For roe deer, we used the pooled number of pellet groups found on both transects in each square, i.e. 40 spots, as a unit (resulting in N = 60, 400 m^2 each), to obtain the best fit to the negative binomial distribution. The negative binomial distribution is described by two parameters: the mean number of pellet groups (m), and a positive exponent (k) (measure of contagion); for details see White & Eberhardt (1980).

Results

Diet investigation by scat analysis

Moose, roe deer, and badger dominated the diet of the wolves, as hair from these three species were found in 52%, 50%, and 19% of the scats, respectively (Table 1; note that hair from more than one species could be found in a single scat). Remains from beavers, hares, and birds were each found in less than 5% of scats. Hair from voles and lemmings were found in 11% of scats (see Table 1), but normally as secondary content and therefore not important as prey for the wolves. Hair from sheep, the only domestic animal we found remains from, occurred in 0.4% of scats (see Table 1). In 4% of scats we found hair from wolf cubs, normally as secondary content. The majority (75%) of these were collected in May each year (the first scat was collected 28 April, the last 16 June), showing that reproduction had occurred. We found remains from more than one prey species in 35% of scats and on average there were remains from 1.39 (S.D. 0.59) species in each scat. Moreover, in the 359 and 341 scats containing hair from moose and roe deer, respectively, adults and juveniles of both species occurred together in 11%.

There were no changes in the composition of prey species between summer and winter (see Table 1). Nevertheless, there were significant differences between summer and winter in the occurrence of hair from juvenile and adult moose, and juvenile roe deer, but not in adult roe deer (see Table 1). However, presented proportions of 'adult' moose and roe deer during winter in Table 1, also includes unknown proportions of young-of-the-year (see Methods).

We found significant between-year differences in the composition of hair from various prey species in the scats ($\chi^2_9 = 24.09$, $P < 0.01$; Fig. 1). However, the frequency of occurrence of moose and roe deer hair was stable throughout the study period, although there was a tendency for moose to be more common the first year (see Fig. 1). The smaller proportion of hair from 'other' prey species (e.g. beaver, hare, rodents, birds), and the higher proportion of hair from badger in the last year of the study contributed most to the significant difference between years (see Fig. 1).

Our calculations suggested that the 684 scats represented a total mass of 915 kg food ingested, all prey species pooled (area/volume ratio adjustments according to Weaver 1993). The three largest species, moose, roe deer, and badger constituted 97% of the mass. Among these three, moose was most important, constituting 66%, whereas roe deer and badger constituted 27% and 8%, respectively (Fig. 2). When back-calculating from assumed prey weights (only

Table 1. Occurrence of hair (or feathers) from various prey species in wolf scats given as proportions (%) and total number (N). Hair from more than one prey species could occur in the same scat.

	Total*		Summer**		Winter***		Season diff.	
	%	(N)	%	(N)	%	(N)	χ^2	P
Moose *Alces alces*	52	(359)	52	(209)	54	(150)	0.13	0.72
Adult	33	(228)	23	(92)	49	(136)	24.97	<0.001
Juvenile	25	(169)	35	(141)	10	(28)	34.06	<0.001
Roe deer *Capreolus capreolus*	50	(341)	51	(208)	47	(130)	0.44	0.51
Adult	44	(303)	41	(168)	48	(134)	1.21	0.27
Juvenile	11	(77)	18	(74)	1	(3)	40.07	<0.001
Badger *Meles meles*	19	(129)	20	(83)	17	(46)	1.11	0.29
Beaver *Castor fiber*	1	(8)	1	(5)	1	(3)		
Hare *Lepus timidus*	2	(14)	2	(7)	3	(7)		
Vole/Lemming *Arvicolinae*	11	(75)	9	(37)	14	(38)		
Domestic sheep *Ovis aries*	0.4	(3)	1	(2)	0.4	(1)		
Bird *Aves*	3	(20)	3	(11)	3	(9)		
Wolf cub *Canis lupus*	4	(25)	4	(17)	3	(8)		

* N = 684 (March 1988 - June 1992)
** N = 406 (10 May - 9 November)
*** N = 278 (10 November - 9 May)

estimated mass consumed included, see Methods) we found roe deer to be the most commonly consumed species by number, constituting 52%, whereas moose and badger were about equally common, constituting 25% and 23%, respectively (see Fig. 2).

We used these proportions by number in an attempt to assess the impact of the wolves on the ungulate populations. However, we have no data on consumed biomass of the wolves in this study. The literature suggests a range of 2 to 8.4 kg of consumed mass/wolf/day (Kolenosky 1972, Peterson 1977, Fuller & Keith 1980, Fritts & Meach 1981, Hollerman & Stephenson 1981, Carbyn 1983, Peterson, Woolington & Bailey 1984, Messier & Crête 1985, Ballard et al. 1987), assuming a mean mass of 40 kg of the wolves in this study (Olsson & Wirtberg, unpubl. data). Restricting the interval to 2.5 to 5 kg/wolf/day, our assessment is that the five wolves annually killed 90-180 roe deer, 45-90 moose, and 40-80 badgers, plus a smaller number of other species. The majority of these wolf-killed ungulates were young animals, because (i) about one third of the roe deer and half of the moose were those with juvenile (reddish) fur killed during summer (judging from proportions of hair in scats and taking prey mass at different age into account), and (ii) in the remaining ones, with 'adult' fur (see Methods), the proportion of young-of-the-year still was high, 50% in moose, judging from the kills found (see next section).

Sex and age of moose killed by wolves vs hunters

During a period of eight years (1985-1992) we found 65 moose killed by wolves; only seven kills of roe deer were found and most of these were so thoroughly consumed that sex and age could not possibly be determined. Being more easily detectable under snow conditions, 80% of moose kills were found during winter (November-April). Sex could be determined in 58 (89%) of the moose kills. Of these, 76% were females (all age classes pooled), which was significantly more ($\chi^2_1 = 9.37$; $P < 0.01$) than the proportion of females (53%) in the sample of moose killed by hunters (total N = 155; all age classes pooled). Moreover, wolves and hunters killed different proportions of the sexes depending on the age of the moose. In the age class 0-2 years, 67% of the wolf-killed moose were females (N = 42, sexes pooled) versus 39% killed by hunters (N = 95, sexes pooled), which is a significant difference ($\chi^2_1 = 8.97$; $P < 0.01$). Of moose ≥ 3 years old, females dominated in both wolf (100%; N = 16) and hunter (77%; N = 57, sexes pooled) kills,

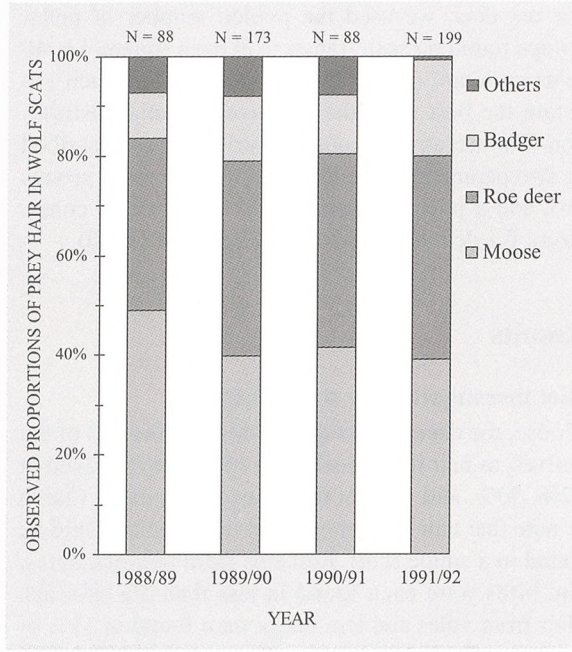


Figure 1. Observed proportions of hair from prey species in wolf scats collected during 1988-1992 in northern Värmland, south-central Scandinavia. The bars show the yearly proportion of moose, roe deer, badger and 'others' based on scats collected from 10 May to 9 May the following year. To keep the data uniform within the 12-month periods 44 and 92 scats collected before the former and after the latter date, respectively, were excluded.

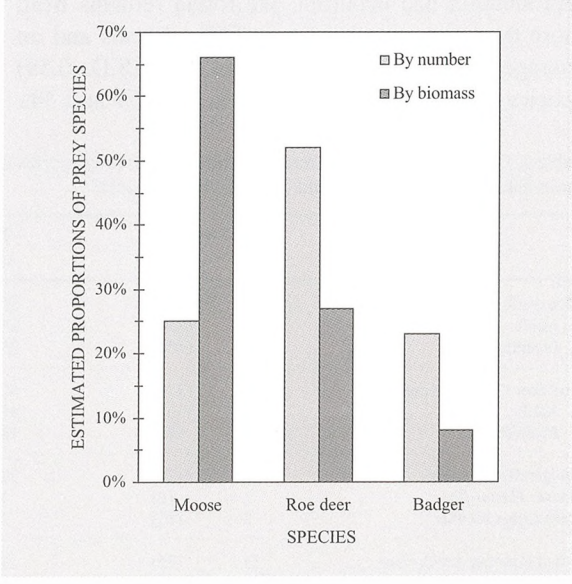


Figure 2. Estimated proportions by number and consumed biomass of the three most important prey species of wolves in south-central Scandinavia. Data are derived from the scat analysis and adjustments are made to different area/volume ratios in animals of different body-size according to Weaver (1993).

but the higher proportion of females killed by wolves was significant ($\chi^2_1 = 4.69$; $P < 0.05$). Accordingly, while wolves killed most females in both young and old moose, hunters changed from males in young to females in old moose.

Of the 65 kills by wolves 51% were calves (<1 year old), whereas 1- and 2-year-old moose together constituted 25% (Fig. 3). The age interval of 3-7 years was poorly represented (5%) in the wolf diet, whereas the interval of 8-12 years was more common (15%). We only found three moose >12 years old to have been killed by wolves, one (1.5%) was 14 years old, and two (3%) were 20 years old (see Fig. 3).

We found no significant differences in the proportion of moose of different age categories killed by wolves and hunters ($\chi^2_2 = 1.47$; $P = 0.48$) (moose were pooled in three age classes: 0-2, 3-11, and >11 years to achieve sufficient numbers for the analysis). To make the comparison more adequate we excluded hunter-killed males that were more than two years old because no moose in this age category were killed by wolves.

We also made a general assessment of disease or deformity in animals killed by wolves and hunters, but found no obvious signs of neither in the two samples.

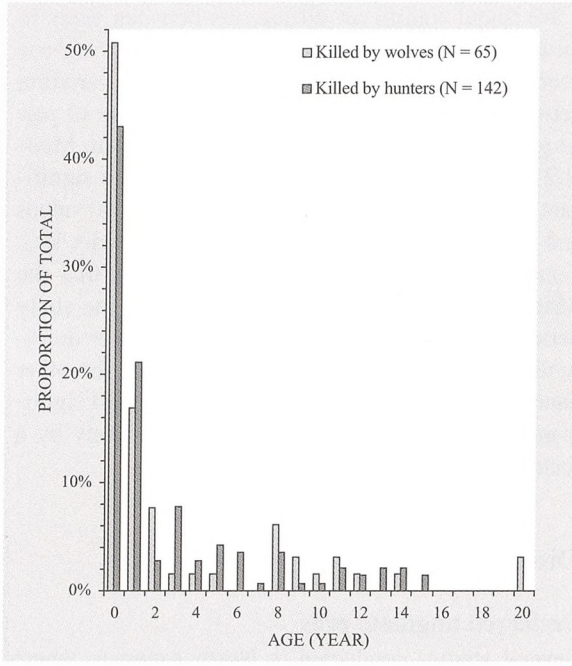


Figure 3. Age distribution of moose killed by wolves and hunters, in south-central Scandinavia. As the wolves did not kill male moose older than two years of age, males of this age category were not included in the sample of hunter-killed moose.

Ungulate census

The estimated mean winter density of moose during the study period was 1.5/km², means ranging from 1.2 to 1.8 animals/km² (Fig. 4). The corresponding roe deer density was considerably lower, 0.4/km², means ranging from 0.2 to 0.7 animals/km² (see Fig. 4). Consequently, assuming that the wolf territory was 600 km² (including the Norwegian side), the mean number of moose and roe deer in winter was 900 (range: 720-1,080) and 240 (range: 120-420), respectively.

Our moose pellet data did not differ significantly from the negative binomial distribution in any of the five years (see goodness-of-fit probabilities in Appendix Ia, Model 1). For roe deer, no significant differences from the negative binomial distribution were found in four of the five years, but a significant difference ($P = 0.036$) was found in 1989/90 (see goodness-of-fit probabilities in Appendix Ib, Model 1). Despite this deviation in one year, we treated pellet data from all years, and for both species, as if negatively binomially distributed in further analyses.

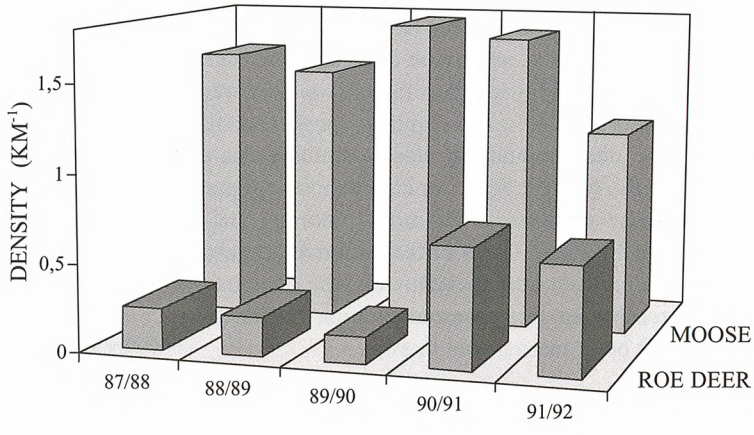


Figure 4. Mean winter densities of moose and roe deer in a 523 km² area corresponding to the wolves' territory. Data are derived from pellet group counts. For a measure of variance, based on mean number of pellet groups each year, see Model 2 in Appendix Ia for moose, and Model 1 in Appendix Ib for roe deer. For statistical analysis of differences between years within both species, see the text, and Appendix IIa and IIb for moose and roe deer, respectively.

We found significant differences between years in mean number of pellet groups for both moose and roe deer. For moose, there was a significant variation between years in mean (m) values of number of pellet groups, but constant k-values; i.e. best fit to Model 2 (Appendix IIa). For roe deer, there were significant variations between years in both mean (m) values and k-values; i.e. best fit to Model 1 (Appendix IIb). Consequently, the biological conclusion is that the winter density of moose decreased during the study period, at least there was a significantly lower density the last winter (1991/92; see Fig 4). On the other hand, the winter density of roe deer increased significantly during the study period, approximately by a factor of 3 (see Fig. 4).

Discussion

Preferred ungulate prey

Several studies conducted in North America, where the general ecological conditions and the body size of wolves are similar to those in Scandinavia, have shown that moose are not preferred when smaller-sized ungulates are available, e.g. white-tailed deer *Odocoileus virginianus* or elk *Cervus elaphus* (Murie 1944, Pimlott, Shannon & Kolenosky 1969, Mech & Frenzel 1971, Voigt, Kolenosky & Pimlott 1976, Carbyn 1983). In our study, the ungulates available for wolves to prey upon were moose and roe deer. Also here the smaller species, the roe deer, was the one most commonly taken. Our data suggest that roe deer were killed about twice as often as moose despite the fact that moose density was about three times as high as that of roe deer. This suggests (i) that roe deer was preferred, and perhaps a more optimal prey, and (ii) that the roe deer population was potentially more affected by the wolves. Still, our calculations suggest that the moose was clearly the most important prey, constituting about two thirds of the total mass ingested, whereas roe deer only constituted about one quarter. The reason for this inverted relationship is the much larger body mass of the moose.

Summer and winter prey

Some studies have reported a change in species composition in the diet of wolf between summer and winter because of easier access to some, often smaller, prey species during the summer, e.g. beaver at Isle Royale (Peterson 1977), whereas other studies have found no notable changes in species composition between seasons, e.g. Peterson et al. (1984). Despite the fact that both beaver and badger, which both are less active during winter, occurred in the territory, we could not detect any significant differences between summer and winter in their occurrence in the diet. Neither could we find any substantial seasonal difference in the proportion of moose and roe deer consumed, although there were probably more roe deer in the territory during summer, due to more pronounced migrations of roe deer in winter towards areas of lower altitude outside the territory. This lack of response may be ascribed to aggregation of overwintering roe deer, e.g. around settlements, thus perhaps making them easier to find despite lower numbers, and that the snow made them comparatively easy to kill in winter compared to moose.

Badgers in the diet

To our knowledge, this is the first study showing that badger constituted a significant part of the diet of wolves; about 8% by mass and 23% by number, corresponding to approximately 45-90 badgers taken by five wolves annually. The relatively large proportion of hair from badgers in wolf scats also in winter did not correspond to the kills found when snow-tracking the wolves; in fact we had only a few indications of wolves hunting for badgers, but no kills were found. The most important reason for this is probably that badgers hibernate when conditions for snow tracking are good, which was only in parts of the mild winters during this study, but another reason could be its smaller size (see next section). We have no estimates on the density of badgers in the territory, and therefore no conclusions on the effect of wolf predation on the population of badgers can be drawn. However, the size and distribution of the badger population in Scandinavia have increased dramatically during the last 150 years, and one reason for this, besides possible climatic changes, may be the corresponding decrease in wolf numbers (Bevanger & Lindström 1995).

Prey found in scats vs tracking

When comparing number of kills found by tracking and the proportions suggested by the scat analysis, a discrepancy between small prey species and moose was consistent for all species. For example, 65 kills of moose but only 7 kills of roe deer were found even though roe deer constituted the largest proportion by number according to our scat analysis. We suggest that this was due to the following methodological rea-

sons: (i) little, or nothing, is left of a kill of a small species, which therefore is more difficult to detect, especially after a snow fall, (ii) the wolves probably stayed for a shorter time at a smaller kill, resulting in fewer tracks in that area, (iii) the killing of small prey species does not attract ravens *Corvus corax*, which were used as indicators when searching for kills, to the same degree as the killing of a large prey species, (iv) we probably tracked wolves in groups proportionally more often than loners, and the former may kill a higher proportion of moose, and (v) to some extent we avoided tracking wolves around settlements, where roe deer seemed to aggregate in winter, and therefore we probably were less likely to find kills of roe deer.

Sex and age of moose killed by wolves vs hunters

Our comparisons of the age and sex of wolf-killed moose to those of hunter-killed moose showed no big differences, even though these mainly refer to the winter period because most kills were found during this season. The only deviation was that the wolves killed a higher proportion of females and no males older than two years. One must, however, bear in mind that both sex ratio and age distribution of the moose population were changed by hunting on beforehand, which influenced what was available for both wolves and hunters, and that the sample killed by hunters probably was biased due to recommendations and preferences by the hunters.

Moose population trend and effects of predation

The number of 900 moose in the territory indicated by our census is a minimum estimate of the annual mean number because it reflects the mean number during winter, thus mainly after the autumn moose hunt (roe deer hunting occurred much less extensively). Hence, when comparing the number of moose in the territory with the estimated number of 45-90 moose killed annually by five wolves, our conclusion is that they killed less than 10%, probably closer to 5%, of the moose population each year. A large proportion of the wolf-killed ungulates were young-of-the-year; more than 50% in moose, probably somewhat less in roe deer.

Hence, the slight decrease in the moose population, found during the last year of our census, is more likely to be explained by other factors, such as hunting quotas, food availability, and/or reproductive success, than by wolf predation. Nevertheless, to be able to maintain a wolf population with the present territory size (see below) in a long-term perspective without a decrease in the density of moose, a slight reduction in hunting quotas, probably around 10-20%, would be appropriate.

It is important to note, however, that there were no other wolf territories in the region. If the wolf population becomes saturated it is likely that the size of the territories will decrease considerably (see e.g. Fritts & Mech 1981). This will result in higher densities of wolves and higher predation on moose. Consequently, there is no serious present conflict with the moose hunters, but there is a possibility of a future conflict.

Roe deer population trend and effects of predation

The tendency of our census to underestimate ungulate density was probably more pronounced for roe deer than for moose. The reasons are (i) that roe deer to a greater extent than moose migrated from the wolf territory during the winters because they are more negatively affected even by moderate snow cover, and (ii) we probably missed areas with aggregations of roe deer because the census was based on relatively few sampling areas, whereas moose were more evenly distributed in winter and therefore more correctly estimated. Moreover, the fact that the sampling area for roe deer pellets covered 40% of the area for moose pellets (see Methods), made the estimate of roe deer density less robust compared to that of moose. Our conclusion is, therefore, that the annual mean number of roe deer was probably significantly higher than the mean number in winter of 240 roe deer estimated in our census. Hence, it is difficult to assess the impact of wolves, which are estimated to kill 90-180 roe deer annually, on the roe deer population. However, it seems obvious that the annual roe deer harvest of wolves constitutes a larger proportion of the roe deer population than the annual moose harvest of the moose population.

Despite this probably significant predation pressure, our ungulate census indicated a threefold increase in the roe deer winter density. One might claim that the wolf territory was a 'sink area' for the roe deer population and that neighbouring areas were 'source areas', supplying the territory with roe deer. However, the situation was complicated by an increasing population of lynx in the region, its density at the end of the study perhaps being as high as 0.5/100 km^2, and their main prey appeared to be roe deer as well (Liberg & Glöersen 1995, pers. obs.).

This suggests that predation by wolves and lynx was more than compensated for by positive factors for the roe deer population, such as the absence of the red fox (due to sarcoptic mange epidemic), and a series of mild winters.

Moreover, we expected to find a functional response from the wolves, i.e. an increasing proportion of roe deer in the diet due to the population increase. However, the proportions of hair from ungulates in wolf scats were relatively stable throughout the study period. We have no explanation for this lack of response, but it may be ascribed to the 'hunting conservatism' of wolves which, has been proposed in other studies (see e.g. Okarma 1995, p. 375).

Acknowledgements - this study was mainly funded by WWF, Sweden, but also by the Swedish Environmental Protection Board and the Swedish Hunters' Association. We are grateful to a number of people for their cooperation, assistance, and advice; especially A. Bjärvall, I. Brelin, K.-Å. Gustavsson, E. Isakson, K. Jonsson, O. Liberg, E. Maartmann, F. Moverare, K. Wallin, and students at Klarälvdalens folkhögskola. We thank A. Johansson, O. Liberg, K. Wahlström and referees for valuable comments on the manuscript.

References

Appleyard, H.M. 1960: Guide to the identification of animal fibres. - Wool Industries Research Association, Leeds, 1-118.

Arnesson-Westerdahl, A. 1987: 12000 år med våra rovdjur. Vargen i vildrenens spår. - Våra rov-djur 1987(3): 22-23. (In Swedish).

Ballard, W.B., Whitman, J.S. & Gardner, C.L. 1987: Ecology of an exploited wolf population in south-central Alaska. - Wildlife Monographs 98: 1-54.

Bergerud, A.T., Wyett, W. & Snider, B. 1983: The role of wolf predation in limiting a moose population. - Journal of Wildlife Management 47: 977-988.

Bevanger, K. & Lindström, E.R. 1995: Distributional history of the European badger Meles meles in Scandinavia during the 20th century. - Annuales Zoologica Fennici 32: 5-9.

Bjärvall, A. 1988: Lär känna vargen: en artmonografi. - Svenska Jägareförbundet, 47 pp. (In Swedish).

Blazej, A. 1989: Atlas of microscopic structures of fur skins. - Elsevier, Amsterdam, 377 pp.

Boyd, D.K., Ream, R.R., Pletscher, D.H. & Fairchild, M.W. 1994: Prey taken by colonizing wolves and hunters in the Glacier National Park area. - Journal of Wildlife Management 58: 289-295.

Brunner, H. & Coman, B. 1974: The identification of mammalian hair. - Inkata Press Proprietary Limited, Melbourne, pp. 1-176.

Carbyn, L.N. 1983: Wolf predation on elk in Riding Mountain National Park, Manitoba. - Journal of Wildlife Management 47: 963-976.

Cederlund, G. & Markgren, G. 1987: The development of the Swedish moose population, 1970-1983. - Swedish Wildlife Research Supplement 1: 55-62.

Ciucci, P., Boitani, L., Pelliccioni, E.R., Rocco, M. & Guy, I. 1996: A comparison of scat-analysis methods to assess the diet of the wolf Canis lupus. - Wildlife Biology 2: 37-48.

Dale, B.W., Adams, L.G. & Bowyer, R.T. 1994: Functional response of wolves preying on barren-ground caribou in a multiple-prey ecosystem. - Journal of Animal Ecology 63: 644-652.

Debrot, S., Fivaz, G., Mermod, C. & Weber, J.-M. 1982: Atlas des poils de mammifères d'europe. - Institut de Zoologie dé l'Université de Neuchâtel, pp. 1-208. (In French).

Floyd, T.J., Mech, L.D. & Jordan, P.A. 1978: Relating wolf scat content to prey consumed. - Journal of Wildlife Management 42: 528-532.

Fritts, S.H. & Mech, L.D. 1981: Dynamics, movements, and feeding ecology of a newly protected wolf population in north-eastern Minnesota. - Wildlife Monographs 80, pp. 1-50.

Fuller, T.K. & Keith. L.B. 1980: Wolf population dynamics and prey relationships in north-eastern Alberta. - Journal of Wildlife Management 44: 583-602.

Gasaway, W.C., Stephenson, R.O., Davis, J.L., Shepherd, P.E.K. & Burris, O.E. 1983: Interrelationship of wolves, prey, and man in interior Alaska. - Wildlife Monographs 88: 1-50.

Hollerman, D.F. & Stephenson, R.D. 1981: Prey selection and consumption by Alaskan wolves in winter. - Journal of Wildlife Management 45: 620-628.

Hörnberg, S. 1995: Moose density related to occurrence and consumption of different forage species in Sweden. - Department of Forest Survey, Swedish Agricultural University, Umeå, Report 58, pp. 1-106.

Jedrzejewski, W., Jedrzejewska, B., Okarma, H. & Ruprecht, A.L. 1992: Wolf prey and snow cover as mortality factors in the ungulate community of the Bialowieza National Park, Poland. - Oecologia 90: 27-36.

Jhala, Y.V. 1993: Predation on blackbuck by wolves in Velavadar National Park, Gujarat, India. - Conservation Biology 7: 874-881.

Kolenosky, G.B. 1972: Wolf predation on wintering deer in east-central Ontario. - Journal of Wildlife Management 36: 357-369.

Kuyt, E. 1972: Food habits and ecology of wolves on barren-ground caribou range in the Northwest Territories. - Canadian Wildlife Service Report Series 21: 1-36.

Liberg, O., Cederlund, G. & Kjellander, P. in press: Population dynamics of roe deer in Sweden: a review of past

and present. - Proceedings of the 3rd International Congress of Game Biology, Edinburgh.

Liberg, O. & Glöersen, G. 1995: Lodjurs- och varginventeringar 1993-1995. - Svenska Jägareförbundet, Uppsala, Viltforum 1995:1, pp. 1-26. (In Swedish).

Lindström, E.R., Andrén, H., Angelstam, P., Cederlund, G., Hörnfeldt, B., Söderberg, L. Lemnell, P.-A., Martinsson, B., Sköld, K. & Swenson, J.E. 1994: Disease reveals the predator: sarcoptic mange, red fox predation, and prey populations. - Ecology 75: 1042-1049.

Linnell, J.D.C., Aanes, R. & Andersen, R. 1995: Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. - Wildlife Biology 1: 209-223.

Markgren, G. 1969: Reproduction of moose in Sweden. - Swedish Wildlife 6: 127-299.

Mech, L.D. 1966: The wolves of Isle Royale. - U.S. Government Printing Office, Washington, D.C., 210 pp.

Mech, L.D. 1970: The wolf: the ecology and behaviour of an endangered species. - The Natural History Press, New York, 384 pp.

Mech, L.D. & Frenzel, L.D. (Eds.) 1971: Ecological studies of the timber wolf in north-eastern Minnesota. - U.S. Forest Service Research Paper NC-52, 52 pp.

Meriggi, A., Brangi, A., Matteucci, C. & Sacchi, O. 1996: The feeding habits of wolves in relation to large prey availability in northern Italy. - Ecography 19: 287-295.

Messier, F. 1991: The significance of limiting and regulating factors on the demography of moose and white-tailed deer. - Journal of Animal Ecology 60: 377-393.

Messier, F. 1994: Ungulate population models with predation: a case study with the North American moose. - Ecology 75: 478-488.

Messier, F. & Crête, M. 1985: Moose-wolf dynamics and the natural regulation of moose populations. - Oecologia 65: 503-512.

Mitchell, B., Rowe, J.J., Ratcliffe, P. & Hinge, M. 1985: Defecation frequency in roe deer (Capreolus capreolus) in relation to the accumulated rates of faecal deposits. - Journal of Zoology, London 207: 1-7.

Murie, A. 1944: The wolves of Mount McKinley. - U.S. National Park Service Fauna Series 5, 238 pp.

Neff, D.J. 1968: The pellet-group count technique for big game trend, census, and distribution: a review. - Journal of Wildlife Management 32: 597-614.

Okarma, H. 1995: The trophic ecology of wolves and their predatory role in ungulate communities of forest ecosystems in Europe. - Acta Theriologica 40: 335-386.

Okarma, H., Jedrzejewska, B., Jedrzejewski, W., Krasinski, Z.A. & Milkowski, L. 1995: The role of predation, snow cover, acorn crop, and man related factors on ungulate mortality in Bialowieza Primeval Forest, Poland. - Acta Theriologica 40: 197-217.

Peterson, R.O. 1977: Wolf ecology and prey relationship on Isle Royale. - U.S. National Park Services Scientific Monograph Series 11, pp. 1-210.

Peterson, R.O., Woolington, J.D. & Bailey, T.N. 1984: Wolves of the Keniai Peninsula, Alaska. - Wildlife Monographs 88, pp. 1-52.

Pimlott, D.H. 1967: Wolf predation and ungulate populations. - American Zoologist 7: 267-278.

Pimlott, D.H., Shannon, J.A. &. Kolenosky, G.B. 1969: The ecology of the timber wolf in Algonquin Provincial Park. - Ontario Department of Lands and Forests Restoration Reproductions (Wildlife) 87, pp. 1-92.

Salvador, A. & Abad, P.L. 1987: Food habits of a wolf population (Canis lupus) in León Province, Spain. - Mammalia 51: 45-52.

Smietana, W. & Klimek, A. 1993: Diet of wolves in the Bieszczady Mountains, Poland. - Acta Theriologica 38: 245-251.

Smith, R.H. 1968: A comparison of several sizes of circular plots for estimating deer pellet-group density. - Journal of Wildlife Management 32: 585-591.

Teerink, B.J. 1991: Hair of West-European mammals atlas and identification key. - Cambridge University Press, Cambridge, pp. 1-224.

Voigt, D.R., Kolenosky, G.B. & Pimlott, D.H. 1976: Changes in summer foods of wolves in central Ontario. - Journal of Wildlife Management 40: 663-668.

Weaver, J.L. 1993: Refining the equation for interpreting prey occurrence in gray wolf scats. - Journal of Wildlife Management 57: 534-538.

White, G.C. & Eberhardt, L.E. 1980: Statistical analysis of deer and elk pellet-group data. - Journal of Wildlife Management 44: 121-131.

Wildman, A.B. 1954: The microscopy of animal textile fibres. - Wool Industries Research Association, Leeds, pp. 1-209.

Appendices

Appendix Ia. Estimates from four models (see Appendix IIa) for moose pellet group counts in south-central Scandinavia. Test of negative binomial distribution (Model 1, goodness-of-fit, GOF, probability) and values of log-likelihood used for test of models in Appendix IIa. For details see White & Eberhardt (1980).

	*m**	Var(m)	*k***	Var(k)	GOF probability	Log-likelihood
Model 1						
1987/88	2.742	0.082	1.055	0.043	0.417	-260.615
1988/89	2.500	0.069	1.073	0.049	0.503	-251.215
1989/90	2.908	0.074	1.417	0.088	0.775	-265.248
1990/91	2.800	0.067	1.499	0.108	0.330	-260.976
1991/92	1.901	0.032	1.802	0.269	0.839	-223.590
Total						-1,261.643
Model 2						
1987/88	2.742	0.071	1.303	0.016	0.857	-1,263.623
1988/89	2.500	0.061				
1989/90	2.908	0.078				
1990/91	2.800	0.074				
1991/92	1.901	0.039				
Model 3						
1987/88	2.561	0.013	1.048	0.043	0.590	-1,267.933
1988/89	1.072	0.049				
1989/90	1.380	0.081				
1990/91	1.478	0.104				
1991/92	1.472	0.143				
Model 4						
All years	2.569	0.013	1.260	0.014	0.547	-1,269.220

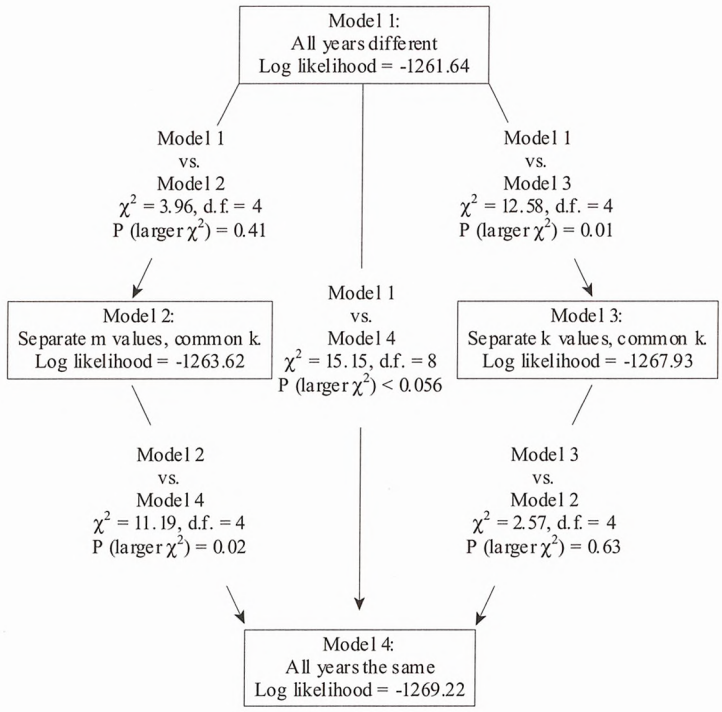
* mean number of pellet groups in each sampling line of 20 spots, see Methods.
** positive exponent in the negative binomial distribution, measure of contagion.

Appendix Ib. Estimates from four models (see Appendix IIb) for roe deer pellet group counts in south-central Scandinavia. Test of negative binomial distribution (Model 1, goodness-of-fit, GOF, probability) and values of log-likelihood used for test of models in Appendix IIb. For details see White & Eberhardt (1980).

	*m**	Var(m)	*k***	Var(k)	GOF probability	Log-likelihood
Model 1						
1987/88	0.483	0.051	0.090	0.002	0.082	-44.582
1988/89	0.450	0.068	0.056	0.001	0.164	-36.318
1989/90	0.283	0.007	0.577	0.262	0.036	-40.499
1990/91	1.150	0.038	1.198	0.285	0.482	-89.015
1991/92	1.200	0.087	0.360	0.015	0.766	-86.781
Total						-297.193
Model 2						
1987/88	0.483	0.021	0.307	0.003	0.002	-313.998
1988/89	0.450	0.019				
1989/90	0.283	0.009				
1990/91	1.150	0.091				
1991/92	1.200	0.098				
Model 3						
1987/88	0.976	0.016	0.076	0.001	0.380	-305.201
1988/89	0.048	0.001				
1989/90	0.152	0.005				
1990/91	1.148	0.252				
1991/92	0.350	0.013				
Model 4						
All years	0.713	0.009	0.249	0.002	0.212	-322.931

* mean number of pellet groups in each sampling area of 40 spots, see Methods.
** positive exponent in the negative binomial distribution, measure of contagion

Appendix IIa. Likelihood ratio tests of four different models describing distributions of moose pellet groups in south-central Scandinavia. Model 2 best fit moose pellet data (see text). Log-likelihood values for different models derive from Appendix Ia.



Appendix IIb. Likelihood ratio tests of four different models describing distributions of roe deer pellet groups in south-central Scandinavia. Model 1 best fit roe deer pellet data (see text). Log-likelihood values for different models derive from Appendix Ib.