

Neonatal Mortality in Roe Deer

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Abstract

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Using radiotelemetry I investigated magnitude and main causes of neonatal mortality of the European roe deer *Capreolus capreolus* in two long-term studies (Ekenäs 1986-1999, Bogesund 1997-2003) in central Sweden. Summer mortality was 51 and 52% in the two areas, respectively, and predation by red fox *Vulpes vulpes* accounted for 88% of the mortality in both areas. Other causes of death were starvation/hypothermia/disease and mowing machines. Potential mowing mortality was, however, estimated to 25-44% during a three-year period, but it was also shown that the use of scaring devices was an effective countermeasure.

Fox abundance was the only factor with significant effect on between-year variation in fawn survival in the 14-year study at Ekenäs. Predation and fawn survival was strongly correlated to fox abundance. High survival during years of low fox abundance suggested that predation mortality was additive during summer. Fawns born just after the birth peak had the lowest predation risk. Predation rate was highest for fawns born very early or very late. Predation thereby seems to strengthen the birth synchrony in roe deer. Contrary to earlier roe deer findings, there was no difference in vulnerability to predation between the sexes. Also differing from earlier findings was that predation rate was highest during the first week of life and declined thereafter almost linearly. Eighty-five percent were killed before 30 days of age and 98% before 40 days. Different types of landscapes may explain the discrepancies between our study and earlier findings. Maternal age or size of maternal home range did not affect fawn survival whereas type of habitat did. Female reproductive success decreased as area open habitat in home range increased, but only during years of high fox abundance. In years when foxes were scarce, females in open habitats had a higher reproductive success, suggesting a trade-off between using habitats of high-quality forage and habitats of low neonatal predation risk. Analyses of fox and roe deer female behaviour supported the hypothesis that it is easier for the fox to find fawns in open habitats. Roe deer females were, however, quite capable to defend fawns attacked by fox, which may affect the fox's hunting strategy.

Keywords: *Capreolus capreolus*, deer population dynamics, generalist predator, juvenile mortality, predator-prey, predator removal, sarcoptic mange, ungulates, *Vulpes vulpes*.

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Appendix

Papers I-V

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

- I. Jarnemo, A. and Liberg, O. Red fox removal and roe deer fawn survival – a 14-year study. *Journal of Wildlife Management*, in press.
- II. Jarnemo, A., Liberg, O., Lockowandt, S., Olsson, A. and Wahlström, K. 2004. Predation by red fox on European roe deer fawns in relation to age, sex, and birth date. *Canadian Journal of Zoology* 82: 416-422.
- III. Jarnemo, A., Kjellander, P., Liberg, O., Månsson, J. and Nordström, J. Trade-off between high-quality forage and neonatal predation risk. Manuscript.
- IV. Jarnemo, A. 2004. Predation processes: Behavioural interactions between red fox and roe deer during the fawning season. *Journal of Ethology* 22: in press.
- V. Jarnemo, A. 2002. Roe deer *Capreolus capreolus* fawns and mowing – mortality rates and countermeasures. *Wildlife Biology* 8: 211-218.

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Introduction

The number of animals in a population is a function of births, deaths, immigrations and emigrations. These fluxes are affected by numerous deterministic and stochastic factors that thus govern changes in population size (Caughley 1977, Tuljapurkar and Caswell 1997). Weather, diseases, habitat, food supply, predation and population density – not only with regard to the population in focus, but also to competing species, predators and their alternative prey – interact with each other. Such factors can limit population growth, but also prevent the population from increasing and even keep the population below certain densities, i.e. regulate the population. An important question is whether different sources of mortality add to total mortality or if a decrease in one source is compensated for by an increase in another, i.e. if mortality is additive or compensatory. The evaluation of such problems requires a careful mapping of a population's mortality patterns. As neonates form potential recruits to the population, analysis of the magnitude, timing and causes of neonatal mortality is central in the study of population dynamics.

Ungulates generally display a classic U-shaped mortality curve with high mortality in the juvenile stages and beyond prime adulthood (Caughley 1966). Predation is by far the most common mortality cause for ungulate neonates. In the presence of predators, neonatal mortality is on average more than doubled compared to predator-free areas (Linnell et al. 1995). Variation in juvenile survival has been suggested to play a predominant role in the population dynamics of large herbivores (Gaillard et al. 1998a,b), emphasising a need for a thorough understanding of neonatal predation. In many cases, it has been shown that predation can be extensive and that neonatal predation can have a strong limiting effect. Yet, the full consequences on the dynamics of the entire population often remain unclear (Boutin 1992, Linnell et al. 1995, Ballard et al. 2001). Little is known about whether the effects are of additive or compensatory nature and if predation is capable of regulating ungulate populations. Several studies imply an additive effect (Beasom 1974, Guthery and Beasom 1977, Stout 1982, Smith et al. 1986, Crête and Jolicœur 1987, Byers 1997a), whereas others indicate that low neonatal summer mortality might be compensated for by high winter mortality (Boutin 1992, Singer et al. 1997). The relationship between population density and habitat carrying capacity appears as one key factor in the study of this problem (Ballard et al. 2001).

The magnitude of neonatal predation suggests that predators can exert a strong selection pressure on ungulates, favouring evolution of antipredatory strategies. Neonatal rearing behaviour and interactions between mother and offspring should thus have been adapted to minimising predation risk. Two main strategies regarding rearing of young can be distinguished in ungulates: the follower and the hider strategy (Lent 1974). In follower species the infant is highly mobile within hours after birth and ready to follow the mother (Rutberg 1984, Shackleton and Haywood 1985). To avoid predation followers rely on fleeing, maternal and group defence, as well as predator swamping. Followers are in general herd-living species inhabiting open areas as opposed to typical hider species that can be

characterised as solitary and living in habitats with dense vegetative cover. Hider neonates spend most of their time hidden and separated from the mother. Depending on species the hiding period varies from a couple of days up to four months (Lent 1974). The mother visits the neonate a few times per day for nursing and changing bed site. The basis for the hider strategy is to avoid detection by eventual predators. Mothers should therefore avoid giving any cues of the location of the hidden young: visits should be limited in number and length and should not be preceded by any particular behaviour (Byers and Byers 1983, FitzGibbon 1993, Thompson 1996).

Several factors have been suggested to affect neonatal predation in ungulates, some of which have also been demonstrated to do so, although results and conclusions sometimes vary between studies (Linnell et al. 1995, Jarnemo 1999). Certain factors may have a direct influence on predation risk, but they may also interact and have an indirect effect through successive reactions. Maternal qualities such as age, experience, condition and habitat choice are likely to affect risk, as are possibly also birth date, sex, condition and age of the neonate. External factors such as climate, habitat, forage and population densities in the predator-prey-system set the frame within which the individual mother and her young can act, and thus affect predation risk directly as well as indirectly. The various factors interact in a more or less complicated web, enhancing the difficulties in evaluating the effects and importance of the single factors.

In this thesis I investigate the neonatal mortality pattern in the European roe deer (*Capreolus capreolus*). In northern Europe, the roe deer is, on the one hand, a valuable game species and, on the other, a major pest species in forest plantations, while in southern Europe it is a species of conservation concern. Hence, this species is of large interest in several respects, emphasising the need for a thorough knowledge of its population ecology in a wide sense (Andersen et al. 1998). The magnitude of mortality is estimated and the main causes of mortality determined. I especially focus on predation by red fox (*Vulpes vulpes*). Apart from the extent of predation, special interest is devoted to various factors that may affect predation. I also try to evaluate and discuss the effects of predation on roe deer population dynamics, although this problem to some extent goes beyond the main scope of this thesis.

Predation by red fox is considered as the most important cause of mortality for roe deer neonates in Scandinavia (Strandgaard 1972, Lindström et al. 1994, Aanes and Andersen 1996). Hence, *Papers I-IV* deal with questions and problems related to fox predation. In *Paper I* the impact of fox predation is studied. The extent of predation is compared to other mortality causes and the relationship between overall fawn survival and fox abundance is investigated. In *Paper II* predation risk is related to age, sex and birth date of roe deer fawns, whereas *Paper III* relates risk to maternal age, habitat choice and home range. By analysis of observations of fox hunting behaviour and interactions between fox and roe deer does, *Paper IV* investigates how the fox finds fawns and how antipredatory behaviour of roe deer females may influence choice of hunting method. That roe deer fawns regularly get killed or injured during mowing is a well-known problem in Sweden, and there is a demand from farmers and hunters for methods to avoid this killing.

However, the magnitude of mowing mortality has not been estimated previously (Linnell et al. 1998b) and although some countermeasures are taken, the efficiency of these methods is unknown. *Paper V* examines the extent of mowing mortality and tests a method to counteract mowing accidents.

The species

The European roe deer is a small cervid with an adult live weight of typically 20-30 kg. Occurring from Scandinavia in the north to the Mediterranean in the south and from Spain and Portugal in the west to the Ural Mountains in the east, the roe deer is the most widespread and common ungulate in Europe. Its habitat requirements are flexible and it is found in a wide variety of environments ranging from deciduous and coniferous forest to shrubland, moorlands, marshes and agricultural plains (Linnell et al. 1998a). It is, however, considered to be adapted to forest habitats of early succession (Liberg and Wahlström 1995). The roe deer is a generalist herbivore, feeding on a broad range of plants, although it prefers herbs and deciduous browse (Duncan et al. 1998). It acts in the manner of a concentrate selector, i.e. being a consumer of high quality food with low fibre content (Hofmann 1985). Although larger groups may form in winter, especially in agricultural areas, roe deer are generally living solitarily or in small groups of two to three individuals composed of an adult female with her fawns, possibly accompanied by an adult male (Hewison et al. 1998). Males defend a territory that is established in spring and held through the rut in July-August (Liberg et al. 1998). Pregnant females seek isolation prior to birth and maintain distance to other females during the breeding season. Females give first birth as two-year-olds and one to three fawns are born in May-June. The birth season is synchronised with 80% of the fawns born during a period of 20-30 days (Gaillard et al. 1993, Linnell 1994, Aanes and Andersen 1996). The maternal postnatal investment and care is extensive and roe deer is regarded as an income breeder (Andersen et al. 2000). The roe deer is a typical hider species (Espmark 1969, Lent 1974) and the fawns lie hidden in vegetation secluded from the mother for most of the time up to an age of about eight weeks (Linnell 1994). The mother visits the fawn 2-7 times a day for nursing and movement to a new bed site. Approximately 10 predator species have been reported to prey upon roe deer, the most important ones being wolf (*Canis lupus*), lynx (*Lynx lynx*) and red fox (Aanes et al. 1998).

The oldest fossil remains of roe deer in Sweden date from approximately 8000 BP. Roe deer immigrated from the south over the land-bridge connecting southern Sweden and Denmark between 10300 and 8200 BP. In historic time its distribution covered the southern third of the Scandinavian Peninsula. From the 16th century and onwards roe deer decreased in range and numbers. The abolishment of the royal and aristocratic hunting monopoly in Sweden in 1789 led to a near extinction and in 1830 the Fennoscandian population consisted of about 100 individuals in southernmost Sweden on the estate of Övedskloster, where they were protected. Other estates joined in the protection and when national hunting restrictions were reintroduced in the 1850s, the roe deer population could expand.

Probably also benefiting from relaxed competition due to a decline in the use of forests for domestic stock grazing, as well as from low predation pressure linked to the near extermination of wolf and lynx, the roe deer recovered quickly and reoccupied its former range over the next 60 years (Cederlund and Liberg 1995). During the 20th century the expansion continued, now additionally favoured by modern forestry and agriculture. Several mild winters, concurrent with a strong decline in fox numbers, resulted in a further increase in number and range in the late 1980s and early 1990s (Lindström et al. 1994). By that time roe deer had reached as far north as 67° N and was only missing on the island of Gotland and in the alpine areas in the north-west (Cederlund and Liberg 1995). Roe deer is, besides moose (*Alces alces*), the most important game species in Sweden. After a peak of 390 000 animals shot in 1993, the annual national hunting bag is now decreasing and was estimated to about 160 000 in 2002 (Kindberg 2003).

The red fox is a medium sized generalist predator with a northern circumpolar range. It is found in nearly all habitat types within its range, living in territorial groups of two to five individuals (Macdonald 1980, Niewold 1980). Two to seven cubs are born in late March to early May. In Scandinavia the most important prey are field voles (*Microtus agrestis*) and bank voles (*Clethrionomys glareolus*), but as the red fox is highly opportunistic, the diet may consist of berries, insects, hares (*Lepus timidus* and *L. europeaus*), rabbits (*Oryctolagus cuniculus*), roe deer, birds, eggs and carrion (Lindström 1982). Both hearing and eyesight are used to localise prey. Voles are caught with a characteristic jump, whereas larger prey are stalked and attacked after a short rush. With an adult weight of 5 to 8 kg, the red fox is predominantly restricted to predation on fawns, although being capable of killing adult roe deer during severe winters (Borg 1970, Cederlund and Lindström 1983).

From the mid 1970's and during the 1980's an epidemic of sarcoptic fox mange spread from north to south in Sweden. Sarcoptic mange is a parasitic skin disease causing terrible suffering for the victims that eventually die from cold and starvation combined with secondary infections in the scratch wounds (Mörner and Christensson 1984, Bornstein et al. 1995). As this was the first outbreak in Sweden in a very long time, the non-resistant fox population was severely reduced.

Study areas

The thesis uses data from two study areas, Ekenäs (*Papers I-II and IV-V*) and Bogesund (*Paper III*), both located in the hemiboreal zone in central Sweden. Both studies were initiated by Olof Liberg, the Ekenäs study in 1986, and the Bogesund study in 1988 (Liberg et al. 1994). Ekenäs is located approximately 100 km south-west of Stockholm (58°58' N, 16°35' E). The core study area covers 300 ha with 53% forest and 47% farmland. The forest mainly consists of managed stands of Norway spruce (*Picea abies*) and Scots Pine (*Pinus silvestris*), but broad-leaved species like alder (*Alnus glutinosa*), aspen (*Populus tremula*), birch (*Betula* spp.) and oak (*Quercus robur*) are common. The farmland is situated in the lower terrain and comprises two-thirds arable land and one-third pasture.

Clover (*Trifolium* spp.) and grass hay, rye (*Secale cereale*), oats (*Avena sativa*), wheat (*Triticum vulgare*) and rape (*Brassica napus*) were the most common crops. The roe deer research project at Ekenäs started in 1986 and was terminated in 1999. At start the population density of roe deer was 10 per km². Within the first three years it increased to 24 per km² and for the rest of the study period density remained relatively stable, varying between 22 and 24 deer per km² (Liberg et al. 1992, Liberg unpubl.). Other larger mammalian herbivores were moose and field and mountain hare. Occasionally a few straying red deer (*Cervus elaphus*) occurred in the area. Besides red fox, other predators recorded in the area were badger (*Meles meles*), pine marten (*Martes martes*) and domestic cat (*Felis catus*). Roe deer hunting was prohibited at Ekenäs during the study period.

The Bogesund area is situated about 10 km north of central Stockholm (59°24' N, 18°12' E). The research area covers 1300 ha and consists of 65% forest, 25% agricultural land and most of the remaining 10% of bogs or bedrock. Dominating tree species are Norway spruce and Scots pine. Common deciduous tree species are aspen, alder, ash (*Fraxinus excelsior*), birch and oak. The agricultural fields are used for production of oats, wheat, rape and hay. Only a minor area of the farmland is used for grazing. The roe deer research project at Bogesund started in 1988. Due to experimental manipulation (Kjellander 2000) the roe deer population density varied during the study period. After an increase from 10.3 deer per km² in April 1989 to 36.1 in September 1992, the population was reduced to 11.4 in 1994. Since 1998 the population has been increasing again and the autumn density in 2003 was 22.1 deer per km². The area also held populations of moose, as well as field and mountain hare. Red fox was the only important fawn predator present, although varying in density because of sarcoptic mange (Lindström and Mörner 1985). Other predators were badger, pine marten and domestic cat. Lynx visited the area only on rare occasions and is not believed to be important for the dynamics of the local roe deer population.

Material and methods

Adult roe deer and juveniles older than five months were caught in box traps during winter. The animals were fitted with radio collars (weight 300g, maximum life span 5 years, Televilt International, Sweden), weighed and recorded as juveniles or adults. For adults caught for the first time, approximate age was estimated by tooth wear (Cederlund et al. 1991). Neonates were found by observing females and waiting for them to visit a fawn, by stalking radio-collared females or by searching surroundings of already radio-marked fawns. At capture the neonates were weighed, sexed and equipped with a radio collar (weight 50g, expanding collar with drop-off function, maximum life span 18 months, Televilt International, Sweden). Radio-marking of neonates was conducted from 1986 to 1999 at Ekenäs and from 1997 to 2003 at Bogesund. Fawn survival was normally checked daily for up to a fawn age of 4-6 weeks, thereafter 1-3 times a week up to an age of 8 weeks. Age and birth date of neonates were estimated by back-calculating, using a weight at birth of 1500g and a daily increase of 150g

(Andersen and Linnell 1998, O. Liberg unpubl.). Deaths suspected to be marking induced were subtracted from the data analysed, as were fawns with failed transmitters. Predation and predator species were established through bite marks and damage on carcasses, buried carcasses and transmitters, carcasses and transmitters found at fox dens, tooth marks on transmitters, bitten off collars and fox-smelling transmitters.

Density of roe deer was determined with the Petersen method (Caughley 1977). The ratios of marked to unmarked roe deer were determined twice a year, in September-October and April-May (Liberg et al. 1992, 1994). All visual observations of foxes were recorded. Observations were not actively sought, but were collected whenever possible during other types of fieldwork. A fox abundance index was constructed by dividing number of fox observations with number of person-days in field during May, June and July. We collected harvest records of red fox and roe deer from 10 larger estates (total area 47,500 ha, range 1,100 to 16,500 ha) in the county of Södermanland, including one estate adjacent to Ekenäs (1,500 ha). Climate data (precipitation, average temperature, and average minimum temperature in April, May and June) were obtained from the nearest weather station (Vingåker), 40 km from Ekenäs.

We analysed mortality and predation rates on fawns using the Mayfield method (Mayfield 1961, 1975, Johnson 1979), commonly used when studying predation on bird nests. This method considers exposure time as it takes into account the number of days ("radio-days") each marked individual is at risk and is especially useful since fawns were born at different times and caught at varying ages. The Mayfield method and the corresponding standard error (Johnson 1979) allow testing whether predation rate differs between two groups, for instance between two age classes, using the normal (z) distribution (Sokal and Rohlf 1995).

The relationship between maternal age and neonatal predation risk was investigated at Bogesund by observing the number of fawns per marked adult female of known age in September. The number of fawns per female in autumn was related to the estimated summer home range of females, in order to investigate the relationship between predation risk and (1) habitat composition and (2) size of maternal home range, respectively. Radio-tracking positions (30 positions per female and summer) were digitalised in a geographic information system (ArcView 3.2). Home ranges were estimated by using the Kernel Home Range method (ArcView 3.2, Animal Movement extension) with ad hoc calculation for the smoothing parameter (H) and with 95% and 50% isoclines. Habitat composition within home ranges was analysed from forestry maps divided in stand units (ArcView 3.2). Agricultural fields, meadows, pastures, clear-cuts, and house lots were classified as open habitats while forest and reed areas were classified as closed.

The study of mortality caused by hay or silage mowing machines was carried out in 1997-1999. Immediately before a planned mowing, the positions of radio marked fawns were checked and those that were bedded in the field to be cut were removed by hand. As these "mowing fawns" were judged to have been killed if not saved by this procedure, their proportion of all radio marked fawns during the entire reproductive season were used as a measure of mowing mortality.

Experiments with scaring devices were performed in June-July 1998 and in May-June 1999. The devices were made of black plastic sacks with a size of 75 x 115cm attached to 2m long wooden poles. An experiment was defined as the instance when an individual female and her fawn or fawns were exposed to scaring devices, regardless of whether the female had one, two or three fawns bedded in the vicinity of the sacks at the start of the experiment. Siblings exposed to sacks in the same experiment were treated individually in the analyses. When marked fawns were bedded in a field, three sacks were set out approximately 100m apart in late afternoon in the part of the field where the fawns were bedded. Although sacks were not deployed all over the field, the idea was to mimic a distribution of one sack per hectare. At this sack density, bedded fawns should not be further away from the nearest sack than 71m. The average distance between the starting positions of the fawns exposed to sacks (referred to as experimental fawns) and the nearest sack was 45m (sd = 15, range 20-80m). The sacks were left out for three days and then removed. Marked fawns not exposed to sacks during the same period were used as control (referred to as control fawns). Siblings in the control set were treated individually in analysis. The positions of the experimental fawns and the control fawns were checked daily in the same manner by visiting the bed sites and observing the fawns. Experimental fawns could be used as control fawns in new experiments.

Results and discussion

Magnitude and causes of neonatal mortality

From 1986 to 1999 233 fawns were caught at Ekenäs (*Papers I and II*). Except for 12 fawns in 1996 that were ear-tagged, all fawns were equipped with radio-collars. After subtraction of deaths that were known or suspected to be capture-induced (n = 9), failing transmitters or disappearance (n = 5) and fawns removed from the area and brought up artificially (n = 3), 216 fawns remained for mortality estimations.

Of the 216 fawns, 113 (52%) died before the age of eight weeks. The by far most common cause of mortality was predation by red fox, accounting for 81% of total mortality and 88% of the known mortality causes (Table 1). Non-predation causes of death were starvation/hypothermia/diseases and hay mowing machines (7% and 5% of known mortality causes, respectively). Ten fawns (9% of total mortality) died from unknown causes. This includes 8 ear-tagged fawns in 1996 for which time and cause of death could not be established, although predation by red fox was the most likely cause.

Magnitude and causes of mortality at Bogesund (*Paper III*) were similar to the results from Ekenäs. During 1997-2003 133 fawns were radio-marked. After removal of capture-induced deaths (n = 2), disappearance (n = 1) and failed transmitters (n = 3), 127 fawns remained for study (Table 2). Sixty-five (51%) of these died before the age of 9 weeks. The dominant cause of mortality was

predation by red fox, which was responsible for 88% of the deaths. Other causes of mortality were starvation/hypothermia/disease (n = 3) and mowing (n = 3). Cause of death could not be established in 2 cases.

The estimated neonatal mortality of 52% and 51%, respectively, is close to the average of 47% in ungulate studies where predators were present (Linnell et al. 1995). That predation was the strongest mortality factor also conforms to the general pattern: when predators are present, they are responsible for the majority of the neonatal deaths. Our results are also similar to those of the only other published study of predation on roe deer neonates (Aanes and Andersen 1996). The belief that red fox is the most important mortality factor for roe deer neonates in Scandinavia (Strandgaard 1972, Lindström et al. 1994) is thereby supported. Whereas starvation/hypothermia is the major cause of mortality in predator-free areas, its magnitude, together with that of diseases and accidents, is reduced in areas with predators. In absence of predators, the average mortality is 19% (Linnell et al. 1995). Looking into the data in the review by Linnell et al. (1995) reveals that when predators are present, known non-predation mortality of marked neonates, i.e. mortality due to starvation/hypothermia, disease or accidents, on average makes up about 10%. This could imply that predators to some extent kill neonates that otherwise would have died from other causes, perhaps further suggesting that unhealthy neonates are more vulnerable to predation. Mortality due to predation could thus, at least partly, be regarded as compensatory in relation to other causes of neonatal mortality.

Although the importance of fox predation was found to be in agreement with other predation studies, its role was perhaps even more prominent than expected. That 88% of the mortality with known causes was due to predation is not exceptional (Linnell et al. 1995), but a predation rate exceeding 85% on three different years is remarkable (Fig. 1). Reviewing 68 studies where predators occurred, Linnell et al. (1995) found no predation rates higher than 85 % and most of them below 60%. Byers (1997a) does however report predation rates of the same magnitude for pronghorn (*Antilocapra americana*).

Mowing mortality – estimates and countermeasures

One mortality cause that is clearly underestimated in the material is mowing since radio-marked fawns in general were removed from the hay-fields prior to cutting. In 1997, 1998 and 1999 potential fawn mortality due to mowing at Ekenäs was estimated to 44, 25 and 25% of the yearly recruitment (*Paper V*). The estimates in my study are comparable to the 26% Kaluzinski (1982) established in Poland and to the loss of 14.5% of the annual hunting bag that Kittler (1979) calculated in West Germany. Mowing mortality thus appears as the second most important mortality factor after fox predation – it might even be of the same magnitude as fox predation. The extent of mowing mortality suggests a strong impact on roe deer population dynamics, at least locally in areas with extensive production of hay and silage. However, without knowing whether this mortality is additive or compensatory in relation to fox predation and other causes of death, the effects on population dynamics remain unclear.

Birth date seemed to affect the risk of being killed, as fawns that were killed or removed were on average born earlier than other fawns. The probable explanation for this is that the earlier a fawn is born, the more likely is it to encounter mowing. The later a fawn is born, the greater the chance that mowing already has been performed in its home range. The risk of an early birth is reinforced as fawns are vulnerable for a relatively long time – fawns were at risk at least up to one month of age and one of the fawns that got killed was 28 days old. The long period of vulnerability, the overlap of the birth and the mowing seasons, and the popularity of hay fields as bed site habitats, interact in causing the pronounced mortality.

During 1998 and 1999, 10 families (14 individual fawns belonging to 10 individual mothers) were exposed to sacks (*Paper V*). In addition to the 10 experiments with first-time exposure, four experiments with families earlier exposed to sacks were conducted (referred to as repeated experiments), comprising a total of 14 experiments. The use of sacks in the fields was found to be surprisingly effective. The day after the sacks were set out, 18 of 22 fawns in the 14 experiments had been removed from the field by the does. This was a significantly higher removal frequency than displayed by fawns otherwise bedded in hay fields. Exposed fawns tended to be removed from the fields to higher extent than control fawns bedded in open habitats and also compared to control fawns irrespective of their type of bedding habitat. After two nights with sacks, 21 of the 22 fawns had been removed. This was a significantly higher removal frequency than for all control fawns and for the control fawns initially bedded in open habitats. Fawns exposed to sacks were also moved a significantly longer distance from the initial bed site than fawns used as control. The distance between the initial bed site by the sacks and next recorded position for the experimental fawns was also significantly longer than the average distance between bed sites of these fawns during the days prior to the experiments.

The results suggest that the sacks had a clearly frightening effect on the roe deer does, and if plastic sacks are left in the field for two nights, almost all fawns will be removed and thereby avoid being killed. The method is cheap and not very time-consuming. One problem is, however, that due to the difficulty to predict weather conditions the decision of when to perform mowing is often taken with short notice. Another disadvantage is that the sacks seem to lose their scaring effect after a couple of days. In two experiments the fawns were back in the field with sacks two days after the start of the experiment and two females had placed their fawns close to the sacks (35 and 60m) on the third day after start. Scaring devices should therefore not be set up too early before mowing. If mowing is postponed they should immediately be taken down.

Factors affecting predation risk

Red fox abundance

The fox population at Ekenäs varied considerably during the study (*Paper I*). The annual fox index varied between 0 and 0.8 observations per person-day (Table 1, Fig. 1) and its validity was supported by the fox harvest on the estate adjacent to Ekenäs. Average daily predation rate over the whole period was 0.026, and varied

between 0 and 0.11 in the different years (Table 1). Predation on fawns and overall fawn survival were strongly correlated with the fox index, whereas there was no significant correlation between fawn survival and roe deer density or any weather factor. A linear regression model of fawn survival against fox index explained 54% of the variation in survival, whereas a negative exponential model explained 56%. The Mayfield-estimated (Mayfield 1961, 1975, Johnson 1979) daily mortality and predation rates (Table 1) were positively correlated with the fox index. Using linear regression models, fox index explained 32% of the variation in the daily mortality rate and 34% of the variation in daily predation rate. Similarly, the Bogesund study (Table 2) showed a strong positive correlation between the annual fox index and predation as well as between the fox index and daily predation rate.

Table 1. Number of marked, dead, and surviving fawns (up to an age of 8 weeks), daily mortality and predation rates, and red fox index at Ekenäs 1986-1999

Year	No. fawns	Fox predation	Other deaths	Surviving fawns	Mortality rate, 10^{-2}	Predation rate, 10^{-2}	Fox index
1986	9	5	-	4	2.3	2.3	0.27
1987	11	-	2	9	0.4	0.0	0
1988	19	-	-	19	0.0	0.0	0
1989	17	-	1	16	0.1	0.0	0.02
1990	12	3	-	9	0.7	0.7	0.01
1991	12	3	4	5	1.7	0.7	0.05
1992	20	12	-	8	2.1	2.1	0.38
1993	19	14	2	3	5.0	4.4	0.14
1994	10	9	-	1	11.0	11.0	0.55
1995	16	14	1	1	7.6	7.1	0.80
1996	19	3	9	7	1.4	1.4	0.79
1997	17	7	2	8	1.7	1.3	0.20
1998	19	7	1	11	1.3	1.1	0.15
1999	16	14	-	2	4.4	4.4	0.69
Σ	216	91	22	103			

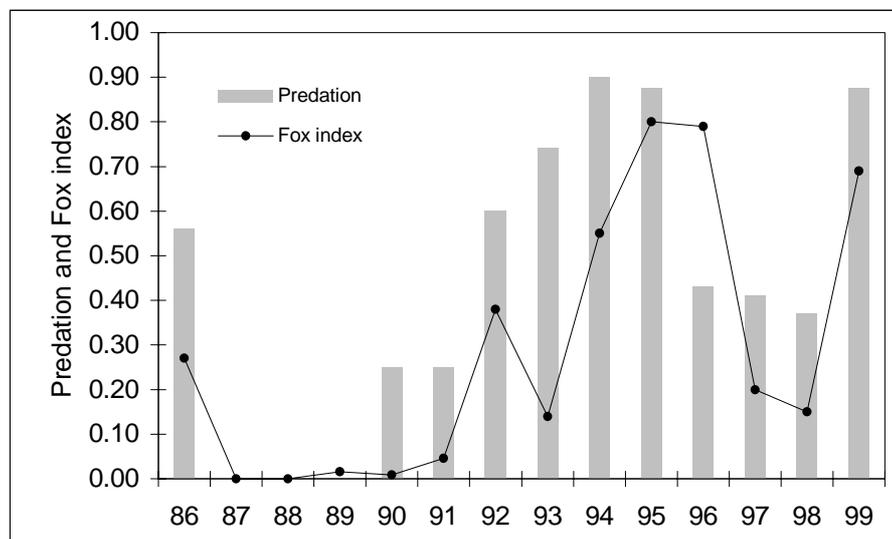


Fig. 1. Predation and fox index at Ekenäs 1986-1999. Note that in 1996, 12 of 19 fawns were ear-tagged and not equipped with transmitters.

The mange epidemic created an efficient natural predator removal experiment to establish the importance of fox density for the survival of roe deer fawns. Both predation rates and total mortality rates tracked the fox population closely,

demonstrating conclusively that fox abundance was the major determinant of fawn survival and the only factor with a significant effect on the between year variation in fawn survival. The strong correlation between the fox index and, respectively, predation and total fawn survival strengthens the conclusion that the fox was the sole predator and that foxes actually killed the fawns and not merely scavenged on them.

Table 2. Number of marked, dead and surviving fawns (up to an age of 9 weeks), daily predation rate and fox index at Bogesund 1997-2003

Year	Marked	Fox predation	Other deaths	Surviving fawns	Predation rate, 10^{-2}	Fox index
1997	12	7	0	5	0.0156	0.25
1998	13	6	2	5	0.0186	0.18
1999	14	6	1	7	0.0125	0.14
2000	19	5	1	13	0.0059	0.14
2001	23	17	3	3	0.0404	0.29
2002	24	10	0	14	0.0101	0.21
2003	22	6	1	15	0.0059	0.16
Σ	127	57	8	62		

Birth date

Mean birth date at Ekenäs (231 fawns) was 2 June \pm 0.7 days, the earliest birth occurred on 21 April and the latest on 7 July (*Paper II*). A peak period in births was distinguished between 25 May and 8 June when 62% of the fawns were born (Fig. 2). Ninety-seven percent of the fawns were born before 20 June.

The synchronised birth period with 62% of the births during 15 days and 79% during 25 days, is similar to earlier findings for roe deer (Gaillard et al. 1993, Linnell 1994, Aanes and Andersen 1996). A concentration of births can be a result of selective pressure due to seasonal variations in climate and food availability (Sadleir 1969, Fretwell 1972), but breeding synchrony is also suggested as an adaptation to decrease predation risk (Darling 1938, Rutberg 1987, Ims 1990a,b). The simultaneous appearance of a large number of young is believed to reduce the per capita predation risk as predators can only catch and consume a limited number of prey per time unit (Darling 1938, Estes 1976, Rutberg 1987). This swamping or saturation of predators should thus increase individual survival chances during the first and most critical stage after birth. Whether synchrony results in swamping and decreased predation may, however, also depend on the type of functional response by the predator and on the spatial structure of the prey population (Ims 1990a,b). For herd-living species, additional antipredatory advantages of synchrony could be group defence against predator attacks (Kruuk 1964, Bergerud 1974, Estes 1976, Estes and Estes 1979) and confusion of the predator as a large number of individuals in a herd or flock can make it harder to catch a specific target (Hamilton 1971).

Earlier studies have supported the general belief that birth synchrony in roe deer is selected for by variations in climate and food resources (Gaillard et al. 1993, Aanes and Andersen 1996). Moreover, as a typical hider species with dispersed and concealed neonates, a better antipredatory strategy for the roe deer should be to breed asynchronously (Rutberg 1987) – a strategy that should especially be favourable when exposed to a switching generalist predator such as the red fox

(Ims 1990a,b, Kjellander and Nordström 2003). The findings at Ekenäs largely support the hypothesis of synchrony as an optimisation to seasonal constraints. If there is an antipredatory benefit from synchrony, the positive effect should be most pronounced among individuals born during the birth peak (Rutberg 1987). This was not the case at Ekenäs. Instead, fawns born during the 15-day period (9-23 June) just after the birth peak had a significantly lower predation risk than fawns born during the peak (25 May-8 June) (Fig. 2). The low predation risk after the peak could, however, be an effect of a low per capita predation risk, as this was the period with the highest abundance of fawns in the vulnerable stage. Thus one could actually say that there was an effect of predator swamping, although slightly delayed and not fitting theory in the predicted manner.

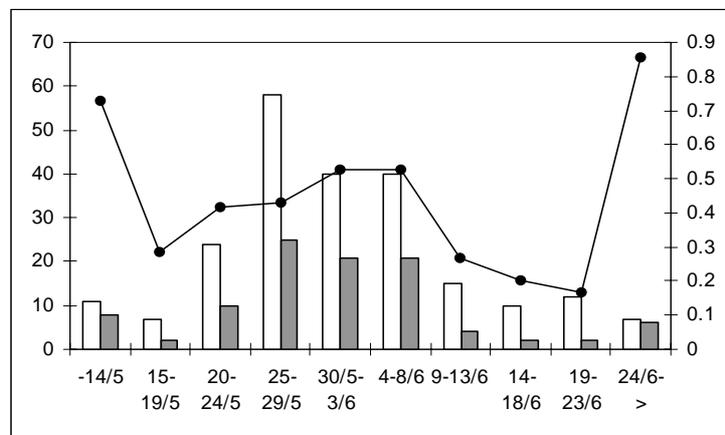


Fig. 2. Birth date and predation risk. Number of born (empty bars, left axes) and killed fawns (grey bars, left axes) in relation to birth date. Predation risk (line, right axes) is expressed as the ratio of killed fawns to born fawns for each time interval.

Predation risk was highest for fawns born in the very beginning or the very end of the birth pulse. A possible explanation is that the number of fawns in vulnerable age classes is low early and late in the season, resulting in a high per capita predation risk. Early-born fawns may have access only to poorly developed vegetation, which increases risk of detection by predators. Harsh weather and insufficient food supply for the lactating mother may further weaken the fawn and make it more vulnerable to predation (Hass 1989). For late fawns the increased risk could be due to the foxes' search image for fawns having improved gradually during the birth season. Late births could, however, also be related to poor maternal condition, which may result in prolonged gestation and delayed births (Verme 1965, Hamilton and Blaxter 1980, Lenvik 1988, Berger 1992, Holst and Allan 1992, Flydal and Reimers 2002, Lambert et al. 2003). Late-born fawns could thus suffer the disadvantage of a mother in poor condition with reduced fawn-rearing capabilities, which would affect survival negatively (Verme 1977, Smith 1987) and possibly also increase predation risk. The high predation rate on early- and late-born individuals implies an enhanced concentration of births and

suggests that the birth synchrony in roe deer not only is due to constraints set by weather conditions and resource availability, but also modified by predation.

Neonatal age

In hider ungulates two different patterns emerge in the relationship between predation risk and neonatal age (Nelson and Woolf 1987). The first pattern is that of high predation from the very start of life, continuing mainly during the first month of life (Cook et al. 1971). A seemingly more common pattern among hider ungulates is characterised by low predation during the first one or two weeks, followed by a hump in predation and hence a higher average age at predation (Barret 1984, Dood 1978, Von Gunten 1978, Bartush and Lewis 1981, Byers and Byers 1983, Epstein et al. 1985, Nelson and Woolf 1987). One explanation suggested for the hump-pattern is that when fawn activity increases with age, the risk of being detected by predators increases (Dood 1978, Nelson and Woolf 1987). The phase when the fawns are changing antipredator strategy from hiding to fleeing could be sensitive, as the fawns are still too young to outrun a predator (Carrol and Brown 1977, Nelson and Woolf 1987). It is also hypothesised that a change in habitat use from denser vegetation for the youngest fawns to more open and riskier habitats for the older fawns could result in this pattern (Aanes and Andersen 1996).

The latter pattern was also found in the only other predation study on roe deer fawns (Aanes and Andersen 1996), where predation was low during the first week and highest from the second to the fourth week. At Ekenäs, however, where age at predation could be established for 86 fawns (*Paper II*), the predation rate was highest during the first week of life (Fig. 3). Predation rate then declined almost linearly with age. There seemed to be a threshold in predation rate at an age of 25 days: a comparison between fawns 21-25 days old and fawns 26-40 days old revealed a significantly lower rate after 25 days. The mean estimated age at predation was 16.4 days and the vast majority of the fox-killed fawns (85%) were 30 days or younger when killed. After the first month, predation was low and after the sixth week negligible – only 2% (2 fawns) were older than 40 days when predated. These observations also differ from Aanes and Andersen's (1996), as 14% of the killed fawns in their study were older than 40 days at death.

The two predation studies on roe deer neonates thus display different patterns in the relation between predation risk and age. A possible explanation for the divergent patterns may be that the type of landscape affects the relationship between age and vulnerability to predation. In areas where forest cover is more extensive, like the one Aanes and Andersen were working in, the fawns are relatively safe during the hiding phase, and it is when they become more active that the predation risk increases. In more open habitats, e.g. in mixed forest/agricultural landscapes like Ekenäs, the fawns seem to be highly susceptible to predation also during the early hiding phase (Nelson and Woolf 1987). The importance of age-specific differences in activity may then be overshadowed by the ease with which predators detect fawns in the open landscape. The almost linearly decreasing predation risk with age found at Ekenäs may just reflect an improving ability to escape from an attacking predator. Alternatively, a forest

landscape highly fragmented by agricultural land may support a higher fox population density (Kurki et al. 1998). During May-June, when the red fox rears its cubs, the foxes' main prey species field vole and bank vole, are at their annual low in density (Hansson 1978, 2002). The presumed high fox density, combined with the scarcity of the foxes' main alternative prey concurrent with the birth of fawns, could lead to an increased predation pressure on fawns (Kjellander and Nordström 2003) and reduce average age at predation.

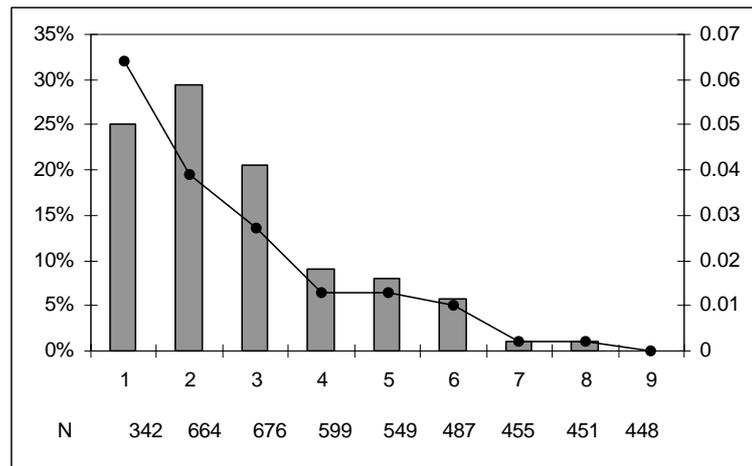


Fig. 3. Age (weeks) and predation risk. Percent killed fawns (bars, left axis) and calculated rate of predation (line, right axis). N is the number of days with radio-marked fawns in each age class. The fox-free years 1987-1989 are excluded.

Sex

The results from Ekenäs also differed from Aanes and Andersen's (1996) in the relationship between predation risk and sex. Whereas the Norwegian study found a male-biased predation risk, there was no effect of sex on vulnerability to fox predation at Ekenäs (*Paper II*). Of 107 males and 109 females, red fox killed 46 (43%) and 45 (41%) respectively.

An unbiased pattern seems to be common for ungulates (Cook et al. 1971, Bartush and Lewis 1981, Trainer et al. 1981, Nelson and Woolf 1987, Ballard 1992, Long et al. 1998, Ricca et al. 2002). However, some studies have reported a male-biased predation (Steigers and Flinders 1980, Mahoney et al. 1990, Franzmann and Schwartz 1986, Smith and Anderson 1996). A higher predation on male fawns is hypothesised to be due to higher male activity (Jackson et al. 1972, Steigers and Flinders 1980). The question then is why predation is not always male biased. Again, habitat differences may offer an explanation for the divergent results. Behavioural differences between male and female white-tailed deer (*Odocoileus virginianus*) fawns starts to appear at the age of three weeks (Schwede et al. 1994). In the white-tailed deer studies conducted in more open landscapes and with lower average age at predation, the majority of the killed fawns did not survive to this age (Cook et al. 1971, Nelson and Woolf 1987),

whereas in the studies performed in more forested landscapes, many of the killed fawns had reached an age where the differences in activity were manifest (Carroll and Brown 1977, Dood 1978, Huegel et al 1985, Nelson and Woolf 1987). A landscape with more vegetative cover thus could increase average age at predation and so generate a sex-biased predation, mediated through sexual differences in activity patterns, which become apparent at a later age.

Habitat composition and size of maternal home range

We found significant effects of the interaction between fox density and area of open habitat on the number of females with ≥ 1 fawn surviving the summer (Fig. 4) as well as of both variables separately (*Paper III*).

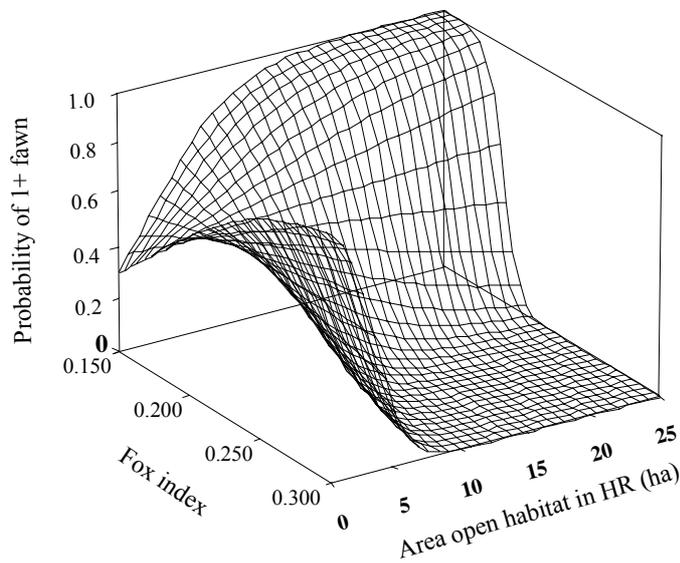


Fig. 4. Probability for a female to have ≥ 1 fawn in September as predicted from fox index and area open habitat in home range. The predicted values were calculated from a logistic regression model with data from Bogesund, Sweden 1997-2003.

Predation risk thus increased with area open habitat in female home range, but only during years with high fox abundance. A higher neonatal predation risk in open habitats seems to be a common pattern for hider ungulates (Beale and Smith 1973, Carroll and Brown 1977, Autenrieth 1980, Barret 1981, Nelson and Woolf 1987, Aanes and Andersen 1996, Canon and Bryant 1997). Aiming at avoiding detection (Lent 1974), the hider strategy seems maladaptive in open habitats. Neonates may be visible over long distances during movements and maternal visits and predators may use the mothers as visual cues in order to locate neonates (Byers and Byers 1983, FitzGibbon 1993, Thompson 1996). Although open habitats also offer some antipredatory advantages – females can extend the distance to the neonate's bed site and still be able to detect and attack approaching

predators (Byers and Byers 1983) – the choice of open habitats for neonatal rearing seems odd for a typical hider species. However, open habitats may be of high quality regarding food, which may balance lower offspring survival during summer. Our study supports this hypothesis. Females with a large proportion of open habitats in their home range had a significantly lower reproductive success than more forest-dwelling individuals in years of high fox abundance, but when foxes were scarce the outcome was the reversed: females using open habitats were then more successful in rearing fawns than females occupying forest habitats. This suggests that there is a trade-off between using habitats of abundant high quality forage and habitats with lower neonatal predation risk. Body mass of roe deer cohorts raised in habitats of high nutritional value is higher than for those raised in poor habitats (Pettorelli et al. 2002) and we suggest this relationship to be the mechanism that possibly can explain the pattern we found.

Maternal home range was used as an indicator of fawn home range and movements. There was, however, no effect of female home range size on the probability of females having ≥ 1 fawn (*Paper III*). Reunion bouts with the mother should from an antipredatory perspective be minimised in time, in number and in the moving distance to reduce detection and predator encounter risk (Ozoga and Verme 1986). From this perspective a larger home range should result in a greater predation risk. However, too much activity in a concentrated area may also put predators on track (Byers 1997b). The relationship between home range size and predation risk is therefore not easy to predict. Further complicating the problem, the type of habitat may affect what strategy is optimal. It is possible that in open habitats the danger of activity in a too restricted area overrules the risk of longer movements.

Maternal age

We found no effect of maternal age or of the interaction between female age and fox density on number of fawns per adult female in September (*Paper III*). Likewise we did not find any difference in number of fawns counted per female in September between the first reproductive attempt in individual females or later in life at ≥ 4 years of age. The hypothesis that predation risk should decrease with increasing maternal age could thereby not be supported.

Ungulate studies showing a direct positive relationship between maternal age and enhanced chances for the offspring to escape predation seem rare. A positive relationship between maternal age and neonatal survival that seems attributable to antipredatory behaviour has been observed in white-tailed deer (Ozoga and Verme 1986, Mech and McRoberts 1990) and in pronghorn (Byers 1997b), indicating that maternal skills improve with age. The roe deer is ecologically equivalent to white-tailed deer and pronghorn, concerning predation on neonates and antipredatory behaviour (Liberg and Wahlström 1995, Byers 1997b, Andersen et al. 1998) and the age-related differences in behaviour and neonatal survival observed among white-tailed deer and pronghorn, respectively, could thus be expected also in roe deer. Actually suggesting this, Kjellander (2000) demonstrated in an earlier study at Bogesund that during years of normal to high fox density, prime-aged female roe deer had a higher reproductive success than 2- and 3-year-olds, whereas there

were no age-related differences in years of unusually low fox density. However, during our study there was just one year (2001) of really high fox abundance and predation. It is possible that the varying abundance of foxes and the importance of habitat obscured the analysis and concealed age-related differences in our study. There is a need for careful experimental and observational studies of maternal rearing behaviour to investigate if females with increasing age and experience behave differently and more cautiously prior to and during reunions with fawns and in relation to fox exposure.

Young roe deer females commonly establish a home range close to or overlapping with their maternal home range (Vincent et al. 1995, Danilkin and Hewison 1996). The habitat composition of a daughter's home range may hence be the same or similar to that of the mother's home range. The quality of the mother's home range might therefore be important for the survival of the daughter's offspring (Gaillard et al. 1998a). Rather than looking for age-specific differences, one should perhaps search for differences between matrilineal groups occupying different habitat types.

Red fox hunting behaviour and defence capabilities of roe deer females

Of 49 encounters between red fox and roe deer females recorded at Ekenäs during 1986-1999, the roe deer attacked the fox in 29 cases (59%) (*Paper IV*). In the remaining encounters the does just observed the fox (14) or reacted either by escape (1) or by keeping a safe distance (5). In 26 of the attacks (90%) the roe deer successfully deterred the fox from the area. In two cases the roe deer female managed to save a fawn attacked by a fox. The aggressiveness of roe deer females influences the fox's choice of hunting method in two ways. First, it should be difficult for the fox to search the surroundings of roe deer females and, secondly, a fox should have small chances of catching a fawn accompanied by its mother. Furthermore, for the red fox it should be important to kill the fawn swift and without vocalisation, otherwise the mother might come running and prevent a successful kill, or prevent the fox from carrying the kill away.

I specifically investigated and compared two hunting methods hypothesised to be used by the fox to find fawns: 1) keeping roe deer females under surveillance waiting for them to visit a fawn, or 2) systematically searching the surroundings of roe deer females or places suitable for bed sites. In the first case the fox might either attack the fawn when together with the mother, or wait until the fawn has bedded and the mother has moved away.

Surveying behaviour – a fox lying, sitting or standing at a point where it had a clear overview over open areas, or moving between such points and now and then stopping to survey, was recorded in 18 observations. In 10 observations, roe deer was observed in the area surveyed. Surveillance often took place from forest edges by the fields (13) and the fox often used boulders to increase overview (8). One of the observed surveys resulted in an attack on a bedded fawn, although the fawn was saved by its mother. In this case the fox observed mother and fawn from a forest edge, waited for the fawn to bed in the field and for the mother to move away, before it approached and attacked the fawn in the bed site. The fact that a

fox seemed to stand little chance against a raging doe implies that it is more profitable for the fox to wait until the fawn has bedded and the mother has moved away.

None of the 28 observed searches resulted in a fawn being found and attacked. In most of the searches (16) the impression was that the fox was not especially searching for fawns, but for any food item. The observations (4) where a fox slowly crossed a clover field in curves or a zigzag-pattern constitute an exception. In the remaining observations (8) the search was possibly directed at fawns. There are two main reasons why the search method appears inefficient. First, the aggressive behaviour of the does, most often resulting in forcing successfully the fox out from the field, should effectively prevent foxes from conducting a thorough search near does. Second, systematic searching of preferred bed site habitats and of the surroundings of females appears uneconomic unless the fox has a hint of where a fawn is bedded (Byers and Byers 1983). The dense and homogeneous vegetation in fields offers an excellent hiding habitat – as long as the fawn is bedded – and gives no clues of preferred bed sites, which might instead be the case in forest habitats (Gaillard and Delorme 1989, Linnell 1994, Andersen et al. 1995). Heterogeneous habitats, with distinct patches offering suitable bed sites, might be more economic to search (Beale and Smith 1973, Autenrieth 1980, Singer et al. 1997). A bedded fawn might be very hard to detect even at a distance of one meter (Linnell 1994, Andersen et al. 1995). Searching the surroundings of roe deer females is probably also too costly. Linnell (1994) recorded a normal distance between 50 and 150 m between the mother and the hidden fawn. Theoretically this means an area of approximately 6 ha for the fox to search. Hence when a fox is searching systematically in a field, it probably has good reasons for doing so, e.g. the suspicion or knowledge that a fawn is hiding in a limited area. It is therefore likely that these systematic searches are preceded by some visual or auditive guidance.

The surveying method seemed more efficient than searching. A fox strategically positioned in the forest edges in the central part of the study area, and perhaps even in elevated positions such as on top of rocks, should be able to survey the open parts of the home ranges of perhaps 2-5 females at the same time. The forest edges may also function as stalking cover (Kunkel 1997) and increase the chances for the fox to remain undetected. The fragmented and to a large extent open landscape of Ekenäs, with forest in the higher terrain and farmland in the lower, could thereby represent an ideal type of landscape for the fox to locate and catch fawns. The possibility to use this sit-and-wait method may provide one explanation for the higher predation risk in open habitats and thus the high predation rates recorded at Ekenäs.

Conclusions and future efforts

Although the Ekenäs study is one of the most comprehensive and longest lasting studies of roe deer fawn survival, we have still not been able to thoroughly establish the role of the fox and its long-term effects on roe deer population

dynamics. The question whether the long-term effect of predation is of additive or compensatory nature is central in ungulate-predator relationships and perhaps the most important for both researchers and managers (Linnell et al. 1995, Ballard et al. 2001). Deer density appears as a key factor, crucial to the impacts of predation (Ballard et al. 2001) and may be responsible for contradictory results among studies whether the effect of predation is additive or compensatory. Populations at or near habitat carrying capacity may respond less to reductions in predation mortality. The high survival of fawns in years of low fox abundance in the Ekenäs study provided evidence that predation mortality was additive during summer. Similar results have been obtained in several other studies, where predators have been experimentally removed (Beasom 1974, Stout 1982, Smith et al. 1986, Crête and Jolicœur 1987, Byers 1997a). When compensatory mortality occurs during the postpartum period, it seems related to high deer density and deteriorated range conditions (Carroll and Brown 1977, Steigers and Flinders 1980, Singer et al. 1997). This is, however, not relevant in the study of Scandinavian roe deer populations. Here the bottleneck is rather the winter, and if reduced neonatal predation mortality will be compensated for, it will most likely be through increased winter losses. Still, the question of an additive or compensatory effect remains unsolved for roe deer as well as for ungulates in general. There is a clear need for large, detailed, long-term studies and/or experimental studies where the effects of ungulate density, predator density, alternative prey, climatic factors, and habitat can be separated (Ballard et al. 2001).

As long as this type of comprehensive study is missing for roe deer, the discussion must be one of assumptions and guesses based on results from various studies. Liberg and Kjellander recorded density dependent effects on body mass, growth, fecundity and survival when density was 30-36 roe deer/km² (Liberg et al. 1994, Kjellander 2000). On a fox-free island, Andersen and Linnell (1998) could not detect any density dependence in fawn summer survival as roe deer population density increased from 10 to 40 deer/km² over a period of 4 years. They did, however, observe an increased proportion of stillbirths and concluded that winter-early spring is a critical period affecting late gestation, whereas good-quality forage is abundant during fawning. In Scandinavia, roe deer therefore will typically show little density dependence in postnatal investment or postnatal mortality (Andersen and Linnell 1997, 1998), strengthening the belief that the effect of fox predation will be additive. During the Ekenäs study, the roe deer population never reached these high densities. It is possible that the mortality from fox predation would generate a less additive effect in a high-density roe deer population subject to density dependent effects, but the compensatory process would in that case most likely act between summer and winter mortality. So far, evidence for the red fox-roe deer system implies additive effects of fox predation (Strandgaard 1972, Liberg et al. 1994, Lindström et al. 1994). The extensive, nationwide increase of roe deer in Sweden during the mange period was most likely related to lower fox predation on roe deer fawns. The national increase of roe deer and the results of the present study indicate a roe deer population density well below habitat carrying capacity at the onset of the mange epidemic. In the Ekenäs study, the enormous impact of the mange on fox density and the strong

effect of fox predation on fawn survival suggest that the driving force in this system was sarcoptic mange.

Although red fox abundance was the factor with greatest effect on annual fawn survival, habitat type also stood out as a key factor. Apart from the direct effect on the fox's hunting strategies, roe deer's antipredatory strategies, neonatal predation risk and female reproductive success, I suggest that the relationship between predation risk and fawn age is affected by type of habitat, and as a result of this, possibly is also the relationship between predation risk and sex. Turning from the habitat composition on a local scale and home range level, what are the effects of the habitat composition on a regional scale? Different types of landscapes with different conditions may form predator-prey systems where the extent and effects of predation differ. In Sweden an interesting comparison would be between northern forest-dominated landscapes and more southern, mixed forest-agricultural landscapes. The former typically harbour relatively low roe deer densities and cycling vole populations (Hansson and Henttonen 1985), whereas the latter are characterised by high roe deer densities (Liberg et al 1994) and low inter-annual variations in vole abundance (Hansson 1978, 2002, Hansson et al. 2000). In the northern systems annual variations in red fox predation on roe deer fawns seems to be closely related to vole abundance as the fox switches from voles to fawns in years when voles are scarce (Kjellander and Nordström 2003). In the mixed landscape, it is possible that the high roe deer density combined with habitats benefiting the fox's search for fawns generate a specialisation on this prey. Further supporting this hypothesis is that fawning is concurrent with the annual low of the fox's main prey species the field vole and the bank vole (Hansson 1978, 2002, Lindström 1982). An alternative approach would be to investigate the importance of roe deer fawns for the fox (Lindström 1994).

The studies at Ekenäs and Bogesund have been of a simple predator-prey system with only one predator species. Currently Sweden is, however, experiencing an increasing and spreading lynx population (Liberg 1998) and a return of the wolf (Wabakken et al. 2001). Locally in southern Sweden there is also an ongoing comeback of the golden eagle (*Aquila chrysaetos*) (Ahlgren 2003). Future studies should also include effects of these more complicated predator-prey systems.

Management implications

The roe deer is abundant and widespread in Scandinavia and fox predation is by no means a threat to the roe deer population. However, fox may suppress the population and decrease potential hunter harvest. Wildlife managers and hunters that want to secure a high yield of roe deer might consider reducing fox density. Our data did not indicate any threshold values in the relationship between fawn survival and fox abundance, but rather a continuous decrease in fawn survival with increasing fox numbers. As roe deer populations in Sweden in general are below densities where density dependent effects may occur, a thorough fox control will most likely result in increased fawn survival and higher potential harvest in any given area, regardless of initial roe deer density.

Hunting efforts of roe deer could be adjusted to fox abundance. Many hunters maintained the high roe deer harvest they had become accustomed to during fox-free years, even after the scabies epidemic had waned and fox populations resurged back to previous high levels. This may have strengthened the decline in roe deer numbers seen in the late 1990s. To achieve an adjustment of hunting pressure to fox levels, wildlife managers and hunters can construct a fox index during early summer, as described in *Paper I*, and estimate a fawn:doe ratio during late summer and early autumn to foresee status and plan potential harvest of the roe deer population.

Mortality caused by mowing machines should not be neglected from a management perspective. It is possible that it sometimes even exceeds that of fox predation. Wildlife managers, hunters and farmers should therefore also consider efforts to hinder the killing and injuring of fawns during mowing.

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