

Temporal and Spatial Variation in Predation on Roe Deer Fawns

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Temporal and Spatial Effects of Predation on Roe Deer Fawn Mortality

Abstract

This thesis deals with variation in mortality of roe deer fawns, over time and in space, caused by red fox and Eurasian lynx predation in a boreal landscape. The thesis considers historic and recent effects of vole population dynamics on red fox predation on roe deer fawns, using long term time series from Grimsö Wildlife Research Area. Historically, the vole population of south-central Sweden has varied cyclically, causing red fox and roe deer fawns to fluctuate synchronically in accordance with the alternative prey hypothesis, but following a dampening of vole cycle amplitude this relationship has ended.

The thesis also covers mortality of roe deer fawns in a multi-predatory context as both red fox and Eurasian lynx are revealed as important predators of roe deer neonates in a study using radio marked fawns. A study on roe deer female habitat choice and survival of fawns points out a possible trade-off in does between high quality forage and survival of fawns.

Weak, but long reaching spatial effects of predation are found as the relation between roe deer fawn survival and distances to fox dens with litters are investigated, and a study on supplemental feeding of red fox as a means of relieving fawns from predation pressure proves this practice futile in boreal forest.

Keywords: predation, roe deer, fawn, red fox, Eurasian lynx, voles, alternative prey, spatial effects, trade-off, supplemental feeding.

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Dedication

To my family.

Det hela är röken bara av en ande som trotsar och ber, det är grått, det är släckt, det försvinner, det är milrök ingenting mer.

Dan Andersson

Contents

List of Publications	7
1 Introduction	9
1.1 Aims	9
1.2 Regulation of prey species	9
1.3 Ungulate Mortality and Predation	11
1.4 Predation on Neonate Ungulates	12
1.5 Boreal Small Game Dynamics	13
1.6 Lifetime Reproductive Success	13
1.7 The Temporal and Spatial Aspects of Predation	14
1.8 Studied Species	15
1.8.1 The Roe Deer	15
1.8.2 The Red Fox	16
1.8.3 Voles	16
1.8.4 The Eurasian Lynx	17
1.9 The Studied Predator - Prey System	17
2 Material and Methods	19
2.1 Study Areas	19
2.2 Roe deer data	20
2.3 Density Estimates of Red Fox and Voles	21
2.4 Supplemental feeding of red fox vixens	22
2.5 Statistical Methods	22
3 Results and Discussion	25
3.1 Roe deer fawns and the Alternative Prey Hypothesis (I)	25
3.2 Roe deer fawns, dwindling vole cycles and lynx predation (II)	28
3.3 Roe deer fawns' landscape of risk (III)	30
3.4 The quality of mothers' home ranges and roe deer fawn survival (IV)	33
3.5 Roe deer fawn survival and additional feeding of red foxes (V)	35
4 Future perspectives	39
References	41
Acknowledgements	50

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List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I Kjellander, P. & Nordström, J. (2003). Cyclic voles prey switching in red fox and roe deer dynamics – a test of the alternative prey hypothesis. *Oikos* 101(2), 338–344.
- II Nordström, J., Kjellander, P., Andrén, H., & Mysterud, A. Roe deer fawn predation revisited – the effects of re-colonizing lynx and dwindling vole cycles (manuscript).
- III Nordström, J., Samelius, G., Mysterud, A., Andrén, H., & Kjellander, P. A den-bound predator creates an extensive ‘landscape of risk’ for roe deer fawns in a boreal landscape (manuscript).
- IV Jarnemo, A. Nordström, J., Kjellander, P., & Månsson, J. Trade-off between high-quality forage and neonatal predation risk in roe deer (manuscript).
- V Nordström, J., Kjellander, P., Andrén, H., & Mysterud, A. (2009). Can supplemental feeding of red foxes *Vulpes vulpes* increase roe deer *Capreolus capreolus* recruitment in the boreal forest? *Wildlife Biology* 15 (2), 222–227.

Papers I and V are reproduced with the permission of the publishers.

The contribution of Jonas Nordström to the papers included in this thesis was as follows:

- I I had little part in long term data collection, but compiled all data. Analyses and writing were made jointly by the authors.
- II I collected and compiled all data, whereas ideas for analyses came from Henrik Andrén, Atle Mysterud and Petter Kjellander, and were performed and interpreted jointly. Writing was made jointly by all authors, but most from my part.
- III I had very little part in long term data collection, but compiled all data. Ideas about analyses came from Henrik Andrén and Atle Mysterud and were performed and interpreted jointly, except GIS work, which was performed by Gustaf Samelius. I wrote most of the text.
- IV I had little part in data collection (one year only), and no part in data compilation, but I did perform modelling and wrote parts of methods, results and discussions of the paper as well as provided improvements to the text.
- V I collected and compiled all data. Ideas about analyses came from Henrik Andrén, Atle Mysterud and Petter Kjellander and were performed and interpreted jointly. I wrote most of the text.

1 Introduction

1.1 Aims

The main aim of this thesis is to quantify the predation, from both red fox and lynx, on roe deer fawns in boreal forest. Further I will investigate the temporal and spatial variation in predation on roe deer fawns and attempt to explain the observed variation by using variables like vole density, predator density, roe deer density, climate and distance to red fox dens. I will compute a possible trade-off in roe deer does between present offspring and females' own survival and future offspring. At last I will present an applied study on supplemental feeding of red fox as a means of increasing survival for roe deer fawns in boreal forest, and share thoughts on future research within this field.

1.2 Regulation of prey species

The size and stability of populations is one of the most important topics in population biology. In prey species, population regulation is thought to be carried out in two different ways: 'bottom-up', where prey are regulated by resources only and reaches their environmental carrying capacity (K), and 'top-down', where predators regulate and stabilize the density of the population below K (Hairston *et al*, 1960; Sinclair, 1995). Of course, predation can occur in both regulatory systems, but in the case of 'bottom-up' regulated populations predation is thought to occur under compensatory forms rather than additive. Errington (1946) introduced the terms additive and compensatory mortality and he strongly advocated the latter, where only weak and sick prey that would otherwise have died from disease are killed by predators.

The view that predators only kill a 'doomed surplus', and that prey populations are regulated mainly by density dependent food limitation, as an effect of intraspecific competition was the dominating opinion during a large part of the last century until finally strongly questioned in the late 20th century (e.g. Erlinge *et al.*, 1984; Erlinge, 1987). From that time onward a number of studies have made it clear that a prey population can be regulated by predation rather than resources under certain circumstances (e.g. Lindström *et al.*, 1994; Sinclair, 1995; Sinclair *et al.*, 2003).

Thus, predation has been found to be a strong regulating factor in certain prey populations, but for a predator species to be able to regulate a prey population a number of demands must be met. The predator must have a potential to respond rapidly by means of numerical and functional response to an increase in prey population density (Holling, 1959a; Holling, 1959b; Holling, 1965) as well as an ability to prevail during a decline in prey density.

In order to survive at times when main prey is scarce, many predators turn their attention to alternative prey species through functional response. The alternative prey hypothesis states that a predator with a strong preference for a main prey that fluctuates in numbers between years, will switch to an alternative prey when the main prey is scarce (Hagen, 1952; Lack, 1954; Hörnfeldt, 1978; Angelstam *et al.*, 1984; 1985; Small *et al.*, 1993). A number of studies found evidence that supported the alternative prey hypothesis and proved that predation can regulate the population size of a prey species (Lindström *et al.*, 1987; Marcström *et al.*, 1988; 1989; Lindström *et al.*, 1994; I).

The shared predation hypothesis also recognize the fact that predators can regulate a prey population but states that predators kill prey unselectively, thus synchronizing population oscillations of sympatric prey species (Norrdahl & Korpimäki, 2000). From the prey point of view, periodic outbreaks are means of escaping top-down regulation and instead becoming resource limited as follows from Holling type III functional response in predators.

The principal difference between alternative prey hypothesis and shared predation hypothesis seems to be that a strong functional response in predators cause low predation on alternative prey during years of high main prey density (possibly with a time lag) in predator prey systems functioning according to the alternative prey hypothesis. On the other hand, in systems where the shared predation hypothesis is applicable, strong numerical response of predators cause high predation pressure on both alternative and main prey simultaneously.

1.3 Ungulate Mortality and Predation

The general pattern of mortality in ungulate species, in absence of predators, is U-shaped with high mortality in juveniles and old animals, whereas animals of prime age typically show low mortality rates (Caughley, 1966). Juveniles are the most sensitive to predation of all age classes and a number of studies show that predators prefer juvenile ungulates, and that juveniles are over-represented in predators' diet as compared to ungulates of other age classes (Carbyn & Trottier, 1987; Mills & Shenk, 1992; Fuller & Kat, 1993; Huggard, 1993; Mattioli *et al.*, 1995; Okarma *et al.*, 1995). An explanation for predators favoring juveniles is that predators often are smaller than the average adult ungulate and that there is a risk involved when a predator tries to kill an adult ungulate that defends itself. There are observations of ungulates harming, injuring, and even killing predators (Mech, 1981; Weaver *et al.*, 1992). Ungulate juveniles on the other hand, are small and relatively harmless to predators, thereby being an 'easy' prey.

Starvation is a major cause of mortality in the old age-classes of ungulates, likely due to dental wear. Wear of teeth makes it increasingly difficult for animals to grind feed and gestation gets disrupted causing animals to die from starvation even though there is no shortage of feed (Gaillard *et al.*, 1993). Thus, ungulates above prime age die from predation, disease and most typically from starvation due to dental wear, and there are several indications of senescence in 'over aged' ungulates (Bérubé *et al.*, 1999; Loison *et al.*, 1999; Catchpole *et al.*, 2000; Mysterud *et al.*, 2001).

Mortality of ungulates is largely density dependent (Jorgenson *et al.*, 1997; Singer *et al.*, 1997; Portier *et al.*, 1998; Kjellander, 2000). At high ungulate densities, food gets scarce and a larger proportion of malnourished animals expose themselves to predators in attempts to find food (McNamara & Houston, 1987). A higher proportion of ungulates starve to death as food resources diminishes, and frequencies of sick animals increases with number of starving individuals (e.g. McNamara & Houston 1987; for a review see Kie, 1999).

A number of diseases affect wild ungulates, for example; foot and mouth disease, tuberculosis, sarcoptic mange, and a range of viral diseases (e.g. Baskin & Danell, 2003). Disease may cause epidemics and effect local populations severely (e.g. Sinclair *et al.*, 1985), but, overall mortality of ungulates caused by disease is generally considered to be low in the presence of predators.

1.4 Predation on Neonate Ungulates

The main anti predator strategies for ungulate neonates are hiding and following (hidiers and followers sensu Lent, 1974; Byers, 1997). In follower species, juveniles try to follow the mother almost instantly after birth. Follower species include the equids, muskox (*Ovibus moschatus*), sheep (*Ovis aries*), large bovines and reindeer (*Rangifer tarandus*). All of these species probably evolved in open landscapes that offered little cover for juveniles (Rutberg, 1984; Shackleton & Haywood, 1985). Moose (*Alces alces*) on the other hand is a follower species living in the boreal forest but has been shown to choose place of birth to maximize cover for the calf in order to avoid predation in the first few days when the calf is too small to follow the mother (Bowyer *et al.*, 1999). In hidiers the juveniles do not follow the mother immediately after birth. Instead, females hide their young the first weeks after birth and keep them in seclusion, visiting them a number of times per day for nursing and caring (e.g. Espmark, 1969). Most cervid species, with reindeer as an exception, as well as a variety of antelopes and gazelles are considered to be hider species (Lent, 1974). Hider species are, in general, linked to forest or other dense habitat which offer shelter for juveniles (Lent, 1974). The main part of juvenile mortality in hider species occur when juveniles are old enough to try to outrun a predator, but still too young to succeed (e.g. Aanes & Andersen, 1996). Another characteristic difference between hidiers and followers, besides habitat, is that hider species in general have a small body size whereas follower species are larger.

A 60% survival rate in mountain goat (*Oreamnus americanus*) kids up to one year of age has been reported. Predation from several predators was the sole natural cause of death (Festa-Bianchet *et al.*, 1994). A Canadian study revealed coyotes (*Canis latrans*) to be a severe predator on fawns of white-tailed deer (*Odocoileus virginianus*) and mule deer (*Odocoileus hemionus*) during autumn (Festa-Bianchet *et al.*, 1994). Coyotes have also been recognized as predators on lambs of bighorn sheep (*Ovis canadensis*). In one study less than 25% survival of the lambs was reported, with 67% of lamb mortality occurring within 3 days of birth (Hass, 1989).

1.5 Boreal Small Game Dynamics

The field of small game species interactions and dynamics has been a subject for many studies in boreal Sweden (e.g Hörnfeldt, 1978; Angelstam *et al.*, 1984; Hörnfeldt *et al.*, 1986; Lindström *et al.*, 1987; 1994; Helldin *et al.*, 2006; Helldin & Danielsson, 2007) and elsewhere in the northern hemisphere (e.g. Krebs *et al.*, 1995; Krebs *et al.*, 2001). Part of this long-term interest from ecologists in dynamics is probably explained by the fact that dynamics tend to change as soon as one or two parameters are altered.

In Scandinavia, and especially within the boreal forest ecosystem, a few crucial parameters have changed in later years. Firstly, there is a reported change in ecosystem dynamics due to recent re-colonization and expansion of large carnivores (Sand *et al.*, 2006) and, secondly, there is a change in the dynamics of voles (Hörnfeldt, 2004; Hörnfeldt *et al.*, 2005). Both these parameters are probably of vital importance to the small game community dynamics and to the ecosystem as a whole. The consequences of these new dynamics are still only partly understood, and many established facts forming the basis for game management therefore need to be re-evaluated in order to foresee trends in small game populations and to supply managers with updated and accurate information

1.6 Lifetime Reproductive Success

Individual differences in juvenile survival are one of the main components that cause variation in lifetime reproductive success among breeding females in birds as well as in mammals (Clutton-Brock *et al.*, 1988). Ungulate males do not take part in parental care, so a successful raise of offspring is dependent on maternal qualities only (Trivers, 1972; Saether & Gordon, 1994). Ungulate neonates are vulnerable to cold and wet weather, starvation, diseases and accidents, but the most common cause of mortality is predation (Linnell *et al.*, 1995).

Therefore, predators are expected to exert a strong selection pressure on ungulate mothers and favor the evolution of a neonatal rearing behavior that will minimize predation risk. Thus, the survival of neonates may be dependent on maternal qualities like physical condition but also age, experience and dominance rank, habitat choice and anti-predatory behavior (Ozoga & Verme, 1986; Smith, 1987; Mech & McRoberts, 1990; Nixon & Etter, 1995; Byers, 1997; Nielsen *et al.*, 2004). In order to maximize lifetime reproductive success, females must also balance investment in

current offspring against own survival and future reproduction (Stearns, 1992).

1.7 The Temporal and Spatial Aspects of Predation

Severity of predation pressure on an ungulate population may vary over time. The reasons for this are numerous. Variation may occur between years as the number of predators or prey varies depending on some extrinsic factor, but also over season as availability of the prey varies. For example Lingle (2000) reports on an increase of deer contents in coyote scats in Canada, as soon as ground squirrels (*Citellus* sp.) starts to hibernate and a decrease of deer contents in scats as soon as ground squirrels again become available to coyotes in spring. Snow conditions in winter may render prey more or less vulnerable to predation (Cederlund & Lindström, 1983). Between years variation in predation pressure can also be because of an outbreak of disease in the predator (Lindström *et al.* 1994).

Predation does not only vary over time but also in space. Habitat heterogeneity may offer sheltered areas where predators cannot reach prey, as for instance steep mountain areas (Murie, 1944), but also areas where predators' hunting is facilitated. Kunkel & Pletscher (2000) found that moose are more vulnerable to wolf predation in valleys than in areas of higher altitude because the thin snow cover in valleys attract moose and cause a local higher moose density that facilitates hunting by wolves (*Canis lupus*). Husseman *et al.* (2003) found wolf kill sites in valley bottoms where prey were hindered in their flight by dense snow, whereas cougar (*Puma concolor*) kill sites were found in open shrub areas where shrub cover made stalking more successful.

Landscape characteristics themselves, either natural or of anthropogenic origin, may also cause a spatial variation in predation. Bergerud (1988) found that a decline in caribou (*Rangifer tarandus caribou*) population density in British Columbia was partly explained by certain forest harvest practices that concentrated caribou in small patches rendering them vulnerable to wolf predation.

Central place foraging behavior of a predator causes a varying predation pressure, which becomes weaker further away from the central place (Stevens & Krebs, 1986), and predator home range boundaries may create refuges for prey as predators avoid areas where they may encounter hostile conspecifics (Hoskinson & Mech, 1976; Mech, 1977; Rogers *et al.*, 1980; Lewis & Murray, 1993).

1.8 Studied Species

1.8.1 The Roe Deer

The roe deer (*Capreolus capreolus*) is a small sized (20–30 kg), widely dispersed (Scandinavian Peninsula – Israel, Portugal – the Ural mountains) concentrate selector (i.e. having a demand for high quality, low fibre food, Hofmann, 1985) with a craving for herbs and deciduous browse (Duncan *et al.*, 1998). It is the most widespread ungulate in Europe because of its flexible habitat requirements, but roe deer are probably originally adapted to forest habitats of earlier succession (Liberg & Wahlström, 1995). The roe deer can also be characterized as a solitary living (Hewison *et al.*, 1998) income breeder (Andersen *et al.*, 2000), with delayed parturition and synchronized birth period (Gaillard *et al.*, 1993; Linnell, 1994; Aanes & Andersen, 1996).

Typically roe deer appear alone or in small groups consisting of a doe with fawn(s) and / or a buck (Hewison *et al.*, 1998). Females' home ranges are overlapping and they do not defend a territory. The buck, on the other hand, defends a territory from spring until the end of the rut, which occur in late July or early August and the males' territory overlaps with a number of females' home ranges (Liberg *et al.* 1998).

Most roe deer fawns are born in late May – early June, with 80 % of the fawns born within 20–30 days (Gaillard *et al.*, 1993; Linnell, 1994; Aanes & Andersen, 1996). Being a typical hider species, roe deer does keep their neonates in seclusion for the first eight weeks, visiting them for nursing 2–7 times a day during this time (Linnell, 1994).

In Sweden, roe deer has been present for at least 10 000 years according to fossil records (Liljegren & Lagerås, 1993). The historic population range was the southern third of Scandinavia. Massive hunting from commoners in Sweden after abolishment of royal and aristocratic hunting monopoly in 1789 (supposedly from fear of a French-inspired revolution) led to the near extinction of the species in Fennoscandia and in 1830 only about 100 animals remained on the private estate Övedskloster in Scania where they were protected. Further protection and new hunting legislation in combination with the near extinction of wolves and Eurasian lynx (*Lynx lynx*) caused the roe deer population to expand throughout the 19th century (Cederlund & Liberg, 1995). The species further expanded in the 20th century probably additionally favored by modern forestry and agriculture. A strong decline in red fox (*Vulpes vulpes*) numbers and a few mild winters caused the Swedish population to explode in the late 1980's and early 1990's (Lindström *et al.*, 1994). By this time roe deer inhabited all

of Sweden but the island of Gotland and the north westernmost mountain areas.

The population peak was reached in 1993, when the national hunting bag was 390 000 animals, but since then a steep decline has been noted and today the national hunting bag is about 100,000 animals (www.jagareforbundet.se/viltet/viltovervakningen/avskjutningsstatistik), partly as a result of predator re-colonization.

1.8.2 The Red Fox

The red fox is a medium-sized generalist and an opportunistic predator inhabiting a circumpolar range. Its diet in Scandinavia consists mainly of voles (*Microtus* sp., *Clethrionomys* sp.) and mice (*Mus* sp.), but also capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*), hares (*Lepus* sp.), roe deer and rabbits (*Oryctolagus cuniculus*) as well as berries, insects, small birds and carrion (Lindström, 1982). Red fox is also a generalist when it comes to habitat requirements and is found in nearly all habitats within its range living in territorial groups of two to five individuals (Macdonald, 1980; Niewold, 1980).

During the summer red fox vixens are den bound predators, raising two to seven cubs and make use of a number of adjacent dens. In times of low densities of large predators red fox have been subject to a meso-predator release in Sweden (Elmhagen & Rushton, 2007), which is a strong evidence of competition among carnivores. It is known that red fox is killed by Eurasian lynx, either for food (Mattison, J. unpublished) or competitor removal (Helldin & Danielsson, 2007).

A grim first outbreak of Sarcoptic mange caused by the mite *Sarcoptes scabiei* caused a near collapse of the Swedish red fox population in the 1970's and 1980's, but since the late 1980's red fox population has recovered in all its former range. According to Lindström et al. (1994), outbreak of sarcoptic mange in red fox at Grimsö Wildlife Research Area during 1983–1989, caused the numbers of roe deer to increase with 30%.

1.8.3 Voles

Field vole (*Microtus agrestis*) and bank vole (*Clethrionomys glareolus*) are the main prey species for red fox in Scandinavia. Population fluctuations of voles in northern and central Sweden have typically been of a cyclic nature during the 20th century, with three to four years between population density peaks.

In later years a circumpolar general decline in vole cycle amplitude has been observed (Kokorev & Kuksov, 2002; Hörnfeldt *et al.*, 2005; Kausrud *et al.*, 2008; III). Several small game species as mountain hare (*Lepus timidus*) and black grouse are known to follow the vole cycles in south-central Sweden as red fox switch to prey on these species when voles are scarce (Angelstam *et al.*, 1985).

1.8.4 The Eurasian Lynx

The Eurasian lynx is a medium-sized felid predator largely specialized in roe deer (Haglund, 1966; Aanes *et al.*, 1998), but capable of killing much larger prey as for instance red deer (*Cervus elaphus*) (Linnell *et al.*, 2001). In reindeer husbandry areas semi-domestic reindeer are considered main prey for lynx (Pedersen *et al.*, 1999; Sunde *et al.*, 2000). Forest grouse are also on the menu as well as hares (Linnell *et al.*, 2001). Roe deer is, however, the main prey for lynx in areas where they co-occur (Nilsen *et al.*, 2009a), and lynx show no preference for any age class of roe deer (Andersen *et al.*, 2007; Nilsen *et al.*, 2009b). In Scandinavia lynx home range size varies between 300-800 km² in females and 600-1400 km² in males (Linnell *et al.*, 2001).

1.9 The Studied Predator - Prey System

In the light of the ongoing changes in vital ecosystem parameters; the re-colonization of large carnivores (Sand *et al.*, 2006) and the lessening of vole cycle amplitude (Hörnfeldt *et al.*, 2005), resulting effects may be anticipated on many trophic levels. Neonate roe deer fawns suffer from high mortality rates due to predation by red fox and mortality rates exhibits a variation between years (Cederlund & Liberg, 1995; Aanes & Andersen, 1996). Between years differences in fawn mortality caused by red fox predation have been proposed to be an effect of prey switching behavior in red fox between microtine voles as their primary prey and roe deer fawns as an alternative prey (Lindström, 1994, Aanes & Andersen, 1996). This prey-switching behavior has also been suggested in other predator-prey systems such as, e.g. coyote, mule deer fawns and microtine voles in North America (Hamlin *et al.*, 1984) and eagle owl (*Bubo bubo*), microtine voles and several small game species in Finland (Korpimäki *et al.*, 1990). In addition, Ural owls (*Strix uralensis*) (Korpimäki *et al.*, 1990) and common buzzards (*Buteo buteo*) shift their diet from voles (main prey) to forest grouse species in the decline and low vole years (Reif *et al.*, 2001). Thus, since red fox is known to be a predator of both roe deer and voles it may also be suspected that these two prey species would fluctuate synchronously, with a time lag in

accordance with alternative prey hypothesis in the same fashion as voles and mountain hare or voles and black grouse as shown by Angelstam *et al.* (1985).

Eurasian lynx kill red fox in South-central Sweden through intraguild predation and it has been proposed that this may affect roe deer fawn survival positively (Helldin *et al.*, 2006). This, however, is built on the assumption that roe deer fawns are not frequently killed by Eurasian lynx. If lynx predation on neonate roe deer fawns is reasonably large and additive to red fox predation, there might not be any positive effects of re-colonization of Eurasian lynx on roe deer survival.

Red fox predation on roe deer fawns in boreal forest is generally linked to vole cycles in accordance with the alternative prey hypothesis (I). Fox density is thereby directly linked to vole density, but high fox predation on fawns occurs lagged one year after a vole peak, especially if it is a year of low vole density (i.e. years with many foxes and very few voles; I). However, from 1989 and onwards, the amplitude of the cycle of voles and other rodents has been dramatically dampened, possibly as an effect of climate change – an observation made also in other parts of Eurasia (Kokorev & Kuksov, 2002; Hörnfeldt *et al.*, 2005; Kausrud *et al.*, 2008; III). If there is a general lack of regular vole peaks, this may be expected to affect red fox predation patterns on roe deer fawns, and alter the relationship between voles, red fox, and roe deer fawns altogether.

2 Material and Methods

2.1 Study Areas

Two study areas are used for the papers of this thesis, Grimsö Wildlife Research Area (I, II, III, V) and Bogesund (IV). Grimsö Wildlife Research Area is located in boreal forest in south-central Sweden (59°40'N, 15°25'E). The area is 130 km² and covered to 74% by mixed conifer forest (Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*)), while bogs, mires, and fens cover 18%. Farmland comprises 3% and lakes and rivers cover 5% of the area. Common deciduous tree species are aspen (*Populus tremula*) and birch (*Betula pubescens*, *Betula pendula*). The landscape is flat with altitude rising from 75 m above sea level in the south to 180 m a. s. l. in the north. For a more detailed description of Grimsö Wildlife Research Area see Swenson & Angelstam (1993). Roe deer population density has been censused by pellet group count since 1977. Red fox population density has been censused since 1973, and red fox numbers were severely reduced by an outbreak of sarcoptic mange 1983–1989 (Lindström *et al.*, 1994). The study area was gradually re-colonized by lynx in the 1990's after more than 30 years of absence and the first lynx litter in the study area was recorded in 1996 (Liberg & Andrén, 2006). Besides red fox and lynx, wolves are severe predators on roe deer, but with unknown impact on roe deer fawns.

The Bogesund Area is located just north of central Stockholm in the hemiboreal zone (59°24'N, 18°12'E). The area is 24 km² and is covered by 65% forest, 25% farmland and the remaining 10% consists of a lake, bogs and bedrock. The dominating tree species are Norway spruce and Scots pine. Common deciduous tree species are aspen, alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), birch and oak (*Quercus robur*). The roe deer research

project on Bogesund started in 1988. Because of experimental manipulation (Kjellander, 2000) the roe deer density has varied greatly between 7.4–36.1 deer per km². Red fox is the only important fawn predator present at Bogesund, although varying in density because of sarcoptic mange (Lindström & Mörner, 1985). Lynx has visited the area only on rare occasions and is not believed to be important for the dynamics of the local roe deer population.

2.2 Roe deer data

Fawn per doe ratios in autumn (September–November) has been recorded since 1977. Personnel at Grimsö Wildlife Research Area reported observations of female roe deer with, or without, fawns as observed by chance while hunting, conducting field work or moving by car on the research area. Observations were noted on a map and summarized weekly.

Adult roe deer and fawns older than 5 months were caught in box traps and fitted with VHF radio transmitter collars (500 g, 5 years maximum battery life, Televilt international, Followit, Sweden) at both Grimsö Wildlife Research Area and Bogesund. All animals were sexed, weighed and aged at marking. All animals were individually marked with different colored ear marks. For adults that were caught for the first time, age was approximated from tooth wear (Cederlund *et al.*, 1991).

Neonate roe deer fawns were captured by hand and fitted with VHF transmitters (Televilt TXH-2) with expanding collars, from May 15 to June 30 during six years (2000–2005) on Grimsö Wildlife Research Area and during seven years (1997–2003) on Bogesund. Most transmitters had a mortality function, but transmitters indicating activity as well as transmitters without special functions were also used in the first two years of the study. Fawns were either caught when radio collared does were stalked or by chance as they were spotted accompanying the doe in open habitats within the research areas. Fawns were weighed to the nearest 0.1 kg, and sexed at marking.

Fawns were radio-tracked daily up to an age of 8 weeks, which reflects the period when roe deer fawns are exposed to predation from red fox (Jarnemo *et al.*, 2004). As fawns reached 8 weeks of age they were monitored once or twice a week until the study period ended 180 days after birth. When a dead fawn was found, the radio-collar was examined for bite marks, and the carcass was flayed and examined for bite marks and/or scratch marks, as well as predator specific feeding patterns determining cause

of death. The surroundings were checked for footprints and scats from predators.

Birth date of fawns was estimated from behavioral data at marking (Jullien *et al.*, 1992), and data on body mass at marking, assuming a daily growth rate of 0.15 kg and a birth weight of 1.5 kg (Linnell, 1994). The arithmetic mean of the two was used to estimate birth date. In some cases, a fawn was only possible to age using a single ageing method. If siblings differed in estimated age, the mean of siblings' estimated ages was used. Date of death equaled date of retrieval for the period with daily radio tracking. Death date for fawns found later in the study period was determined using mean date between last date when fawns were recorded to be alive and the date of retrieval. Fawn mortality was estimated by Kaplan-Meier method (Pollock *et al.*, 1989), for the first 180 days of age on the pooled data from all years. Although fawns were born on different dates and in different years, estimated birth-date was set as day 1 for all fawns in survival calculations. Pellet group count has been carried out since 1977, using a defecation rate of 22 pellet groups per day (Neff, 1968; Mitchell *et al.* 1985).

2.3 Density Estimates of Red Fox and Voles

The number of breeding fox vixens was determined by census of all known den sites (N=201) within the Grimsö Wildlife Research Area in early July each year 1973–2005. Presence of a vixen with dependent cubs was indicated by cub scats and remains of prey items. Number of fox litters within the research area ranged between 0 and 11 during this period. This index was used as an estimation of population density in voles each year. At Bogesund a red fox abundance index was estimated as the number of red fox observed divided by the number of person-days in field during May, June and July.

A vole index was estimated at Grimsö Wildlife Research Area by yearly spring snap trapping. In total, about 950 snap traps were distributed systematically on Grimsö Wildlife Research Area in 20 sample areas (1 ha), with about 50 traps in each area and 10 traps at each trapping plot (3,14 m²), and set out for three nights every year. The number of trapping plots varied slightly between areas because some areas contained lakes. Trapping plots were chosen within the sample areas as the best spots available for vole catching, e.g. close to a rock or a tree stump, and were not necessarily situated at exactly the same place every year. The bait used was a

combination of dried fruit and 'Polish wicks', i.e. pieces of woolen yarn dipped in vegetable oil.

2.4 Supplemental feeding of red fox vixens

For the purposes of study (V) Grimsö Wildlife Research Area was divided into a northern and a southern part of about the same size (65 km²) to mimic a large hunting area. The northern and southern area was used as study area in two consecutive years (2004–2005). No den sites were visited before the study took place to determine whether it contained a fox litter or not, because red fox vixens are likely to abandon their den site when disturbed. Therefore we established feeding plots close to den sites where there were most likely that a fox litter would be born based on their popularities as den sites in previous years. Five feeding plots were used in the northern part (2004) and six in the southern part (2005).

Meat from pig (*Sus scrofa domesticus*), moose and roe deer was placed on sand-beds (about 1 m²) for detection of red foxes' and other scavengers' tracks. We placed out a 'large amount' of meat (roughly 20 kg per feeding plot and week) so that over-abundance of food would be secured if foxes regularly visited the feeding plots or if other scavengers competed for the meat. To avoid a numerical response in red foxes, e.g. an increase in number of fox territories or increased litter size, we kept the period of feeding as short as possible. In 2005 feeding started earlier in order to further assure high fox use of feeding plots at birth of roe deer fawns.

The feeding started May 5 (2004) and April 15 (2005), and ended June 24 (2004) and June 23 (2005). Feeding plots were visited twice weekly and the percentage of meat consumed from last visit was then estimated and replaced. When fox tracks or scats were found on the sand bed, as well as when the sand smelled of fox urine, we concluded that foxes had visited the feeding plots and carried away and consumed the missing food. If tracks were erased by rainfall, but bones were missing we concluded that foxes had visited the plots.

2.5 Statistical Methods

In paper I, I used stepwise multiple regression models to analyze effects of cyclic voles and red fox in accordance with the alternative prey hypothesis on roe deer fawn survival, but in paper II–V, I used general linear models

models built on the R platform (R version 2.3.0 – 2.10.0, R development core team 2006 - 2009) to investigate effects of lynx predation, distance to fox dens, and supplemental feeding of red fox on fawn survival, as well as to detect a trade-off between mothers' nutrition and fawn survival.

3 Results and Discussion

3.1 Roe deer fawns and the Alternative Prey Hypothesis (I)

Roe deer fawns were found to act as an alternative food source for red fox in years of low vole population density in accordance with the alternative prey hypothesis (Hagen, 1952; Lack, 1954; Hörnfeldt, 1978; Angelstam *et al.*, 1984; 1985; Small *et al.*, 1993; I).

In paper (I) a negative relationship between red fox litters in spring and ratio of roe deer fawns per doe observed in autumn in the following year (i.e. with a time lag of a year and a half) was found (Figure 1.). This relationship was most evident in years of low vole numbers. Red fox followed the vole cycles without a time lag as predicted and previously observed on Grimsö Wildlife Research Area (Hörnfeldt, 1978; Angelstam *et al.*, 1984; 1985). The time lag of the relation between high recruitment in red fox and low number of observed fawns per doe was explained by vole population dynamics. If vole index was high, red fox responded numerically by increasing their reproductive output; more fox litters were born. In the next year there were many, now adult, foxes on the study area, and if this happened to be a year of low vole population density, these foxes had to turn to other food sources besides voles. In such years, predation on roe deer fawns became intense and resulted in a low fawn per doe quota in autumn.

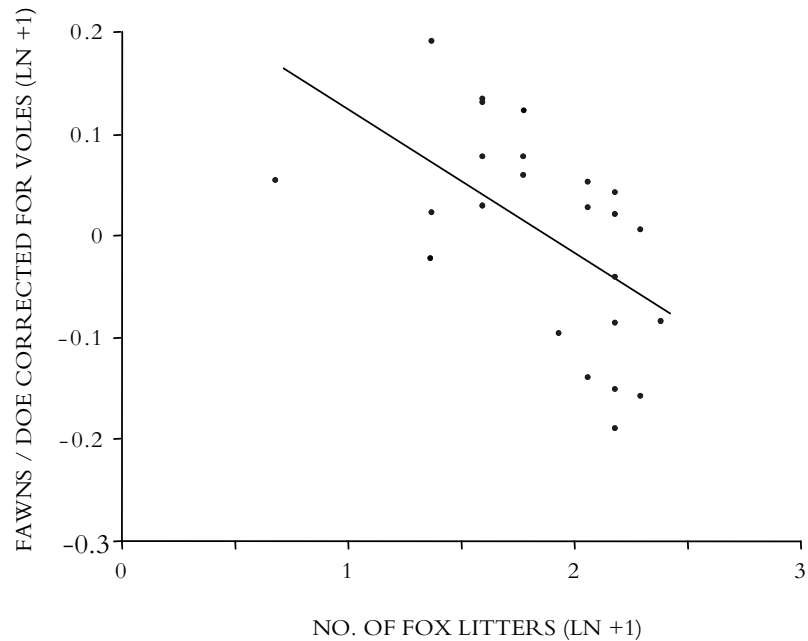


Figure 1. The relationship between fawns per doe ratio and number of fox litters in the previous year. Fawns per doe ratios were corrected for the effects of vole density using the residual variation from the regression between fawn per doe ratio in autumn a year and a half later versus vole density, on the Grimsö Wildlife Research Area 1977–2000.

The red foxes thus showed a functional response from their main prey, voles, to an alternative prey, roe deer fawns. This was interpreted as a support for the alternative prey hypothesis rather than the contesting shared prey hypothesis as no significant relationship was found between densities of predator and alternative prey in the same year. The fawn per doe ratio is a crude measure of roe deer recruitment but it is strongly related to the number of fawns per radio marked roe deer doe (I). Snow depth in the previous winter was found to affect number of fox litters negatively, probably by lowered condition in vixens, but no effects of severe winters was found on roe deer recruitment, even though an earlier study indicated delayed first reproduction in roe deer does (Lindström *et al.*, 1994). Sarcoptic mange could explain a substantial part of the variation in roe deer recruitment by effectively lowering red fox recruitment between 1983 and 1989.

This study also revealed lowered amplitude in vole cycles from 1990 and onwards, that possibly might result from milder winters (Figure 2.). Vole population density is negatively affected by thin snow cover possibly due to greater predation pressure (Lindström & Hörnfeldt, 1994). This phenomenon is not restricted to South-central Sweden or to Scandinavia but seems to be a circumpolar experience (Kokorev & Kuksov, 2002; Hörnfeldt *et al.*, 2005; Kausrud *et al.*, 2008).

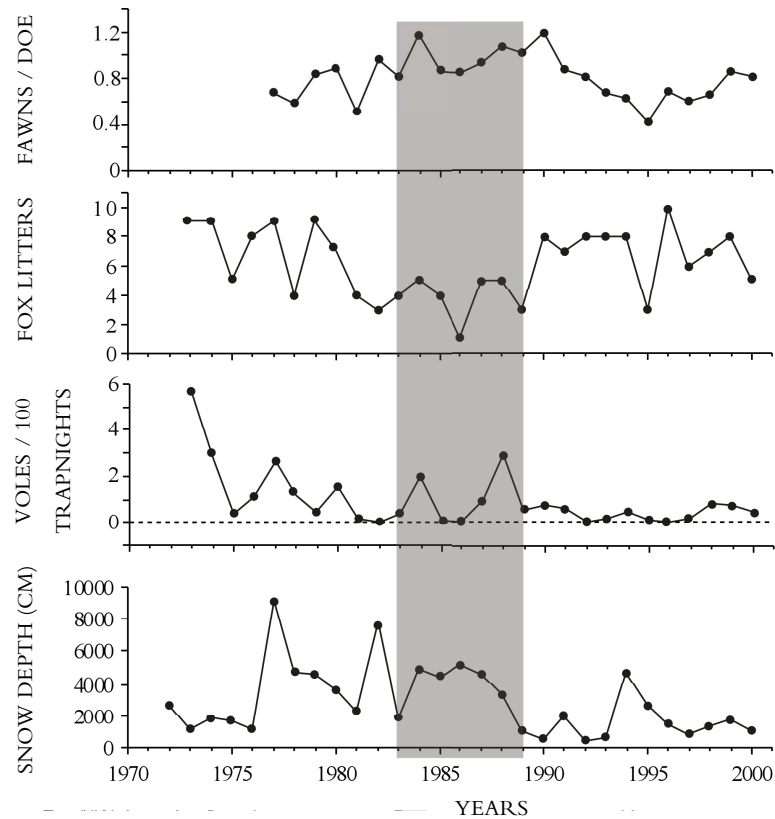


Figure 2. Fluctuations in roe deer fawns per doe in autumn, number of red fox litters, vole index, and summed value of snow depth 1973–2000, on the Grimsö Wildlife Research Area. Years of a sarcoptic mange outbreak are shaded. Note the low vole numbers after 1990.

3.2 Roe deer fawns, dwindling vole cycles and lynx predation (II)

If there is a general lack of vole peaks as noted in paper I, this might strongly affect the observed pattern in the relations between red foxes, voles and roe deer fawns. Another, possibly confounding, factor that needed investigation was the predation impact of re-colonizing Eurasian lynx. Roe deer is the main prey for lynx wherever they co-occur (Nilsen *et al.*, 2009a), and we suspected lynx to be a previously neglected predator on roe deer neonates, especially as lynx show no preference for any other age class of roe deer (Nilsen *et al.*, 2009b).

Therefore, in order to get a better estimate on roe deer fawn mortality and its causes, 101 fawns were caught and fitted with radio collars in 2000–2005 on Grimsö Wildlife Research Area. Total predator caused fawn mortality in boreal forest was 28% in this study (II). Red fox predation caused 16% mortality and Eurasian lynx 13%. Red fox predation was low in this study as compared to other studies from more agriculturally dominated areas (42%, Jarnemo *et al.*, 2004; 25%, Panzacchi *et al.*, 2008), but lynx predation on roe deer neonates was surprisingly high. When modeled, fate of fawns (i.e. killed by predator or survived until the age of six months) was mainly determined by physical condition of the fawn (as expressed by residuals from age at capture and body mass at capture). The vole population density index was no longer an important determinant for roe deer fawn survival as in paper (I).

We believe this is partly because of the observed low vole cycle amplitude and partly because of the return of the Eurasian lynx as a major predator on roe deer fawns. The importance of roe deer fawn physical condition for predation related mortality can largely be explained by the restraints of red fox as a predator. Red fox rarely kill fawns with an age exceeding 58 days (Jarnemo *et al.*, 2004) or a body mass exceeding six kg. Therefore, a fawn that is caught and collared at an age close to 58 days or a fawn that is heavy for its age will have a survival advantage in the study, as compared to those fawns that are caught when very young or small for their age. Thus, large fawns or fawns in good physical condition will experience a shorter time exposed to red fox predation in our study. Spatial separation in predation from red fox and lynx is presented in Figure 3.

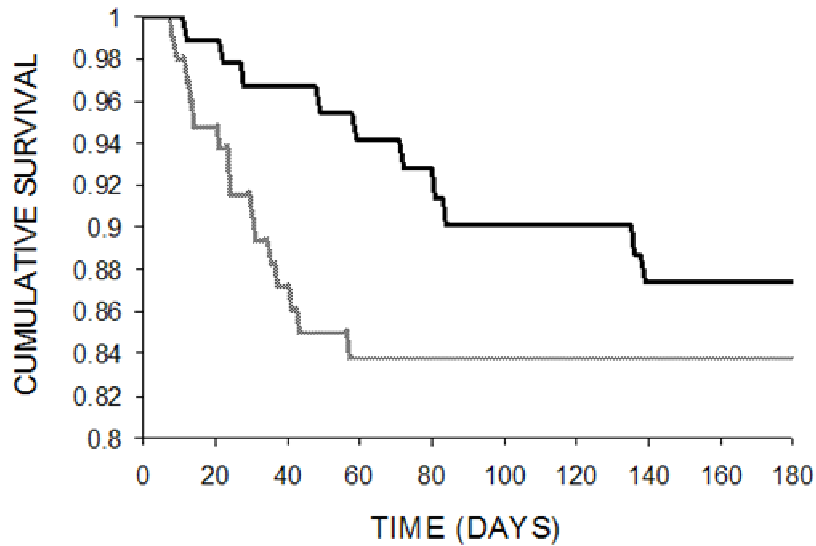


Figure 3. Temporal separation in predation pattern of lynx (black line) and red fox (grey line) during the first 6 months in life of roe deer fawns within Grimsö Wildlife Research Area 2000-2005.

Eurasian lynx predation was thus revealed as a major cause of mortality for neonate roe deer fawns in boreal Sweden. The magnitude of lynx predation makes lynx equally important for roe deer recruitment as red fox predation. It has been argued that the re-colonization of Eurasian lynx may prove beneficial for roe deer populations of boreal Sweden as lynxes also kill foxes through intra-guild predation (Helldin *et al.*, 2006), but this proposal is built on the assumption that very few roe deer fawns are killed by Eurasian lynx. The combined predation pressure of red fox and Eurasian lynx (28%) on roe deer fawns in boreal forest more or less equals the predation pressure by red fox alone in some studies from agricultural areas (Panzacchi *et al.*, 2008), but the lynx will continue to kill roe deer of all other age classes as well, so lynx will pose a potential threat to individual roe deer from birth to old age, and thereby have a strong restraining effect on roe deer population growth in boreal forest.

3.3 Roe deer fawns' landscape of risk (III)

Spatial coincidence shapes species interactions in many different ways (Lewis and Murray, 1993; Schauber, 2000; Schmidt *et al.*, 2001; Schmidt & Ostfeld, 2003). One of the best ways for an individual to avoid death by predation is to occupy a home range without any predators, but such areas are hard to find.

Central place foraging predators may be restricted by the distance they are willing to carry a large prey back to the central place (Stevens & Krebs 1986) and the optimal foraging theory (Schoener, 1979) states that single prey loaders should minimize energy losses by bringing larger prey to the den while consuming smaller prey on the spot. Because of this, Skogland (1991) suggested that den-bound, territorial predators have limited ability to limit ungulate populations.

Furthermore, predators in areas that are fully occupied (i.e. where predators have adjacent home ranges) may avoid intense usage of the parts of their home range that is close to home range boundaries in order to minimize risk of hostile encounters with neighbors (Lewis & Murray, 1993). This behavior can create boundary zones of low predator activity, in which prey may seek refuge (Hoskinson & Mech, 1976; Mech, 1977; Lewis & Murray 1993).

In order to find out whether or not there are any such refuges for roe deer fawns in the boreal forest we used 27 years of data from Grimsö Wildlife Research Area on observations of roe deer does with or without fawns, and yearly locations of red fox dens. Other variables were week of observation, vole density index, accumulated snow depth, years with and without presence of lynx and roe deer density. Average recruitment for all observations during the whole study period was $0.86 \pm \text{S.E. } 0.022$ fawns per doe ($n = 1724$).

The best model to explain the variation in number of fawns per doe included the variables: week of observation, mean distance to all inhabited fox dens, fox density index in the previous year, fox density index in the same year, vole density index and roe deer density index (IV). There were no significant interactions between fox index in the previous year or fox density in the current year and roe deer density. In the best model number of fawns per doe increased with mean distance to the closest den and vole density, whereas fawns per doe decreased with fox density index in the previous year, fox density index, and roe deer density index.

To illustrate the “landscape of risk” for roe deer fawns we constructed a variable “predation risk” by using the Kernel function in Hawth's analysis tools of ArcGis on inhabited red fox dens (Figure 4.).

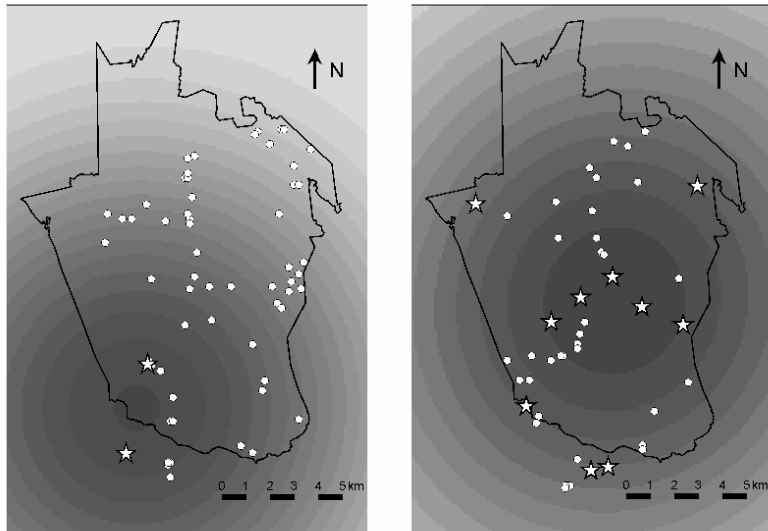


Figure 2. A representation of the landscape of risk for red fox predation on roe deer fawns during two contrasting years using a distance- and density- based measure of risk of red fox predation based on a kernel of fox dens with smoother 16,000. In 1989 (left) only two fox litters (stars) were born on Grimsö Wildlife Research Area (black outline), both in the south western corner of the study area, and in 1992 (right) 10 litters were born, scattered over the entire study area. White dots are observations of roe deer does during the focal year. Risk values are continuously decreasing from a den, but for illustrational purposes they are divided into intervals with units of 0.0002 in this figure. Note that effects of dens outside the study area are unknown.

From the resulting maps we measured an increased risk on roe deer does with fawns up to at least 10 km from an active red fox den. We present in this study the first ever attempt to picture the ‘landscape of risk’ for neonate roe deer fawns in relation to red fox predation.

The emerging picture is grim, as red fox predation risk covers most of the landscape. In addition, fox dens with litters outside the study area will affect roe deer does with a home range near borders of the study area. This study showed a positive effect of increasing mean distances to fox dens on number of roe deer fawns per doe along with the expected negative effects of red fox density with a time lag as well as red fox density in the same year

and positive effects of vole density in the same year (Kjellander & Nordström, 2003). However, the most interesting result is the very weak contrast in spatial risk relative to distance to fox dens with litters even in years when only two dens were active.

We did not find any evidence for the hypothesis by Skogland (1991) that den bound predators are restricted to hunting close by the den. Conversely, results imply that red fox vixens with dependent cubs are willing to roam very far from the den in order to hunt roe deer fawns. This result was also implied in paper (V) where red fox vixens brought supplemental food to the den from feeding plots up to 8 kilometers away. The number of fawns per female increased moderately, but significantly from fox den and outwards for several kilometers. This might also be an effect of other foxes hunting, for example resident males or “floaters” (i.e. non-resident foxes). There is however no doubt that red fox are, or have been, an important factor for roe deer survival as annual variation in the number of fox litters in previous year correlates well with number of fawns per doe (I). The weak effect of distance does not occur because fawns are not killed by red foxes (II), but more likely either red fox vixens have much larger foraging areas around their dens than expected or non-territorial foxes play a larger role for predation of roe deer fawns than assumed (Lindström, 1994). The spatial scale of our study area (130 km²) was not large enough to exactly find the scale of impact, and we do not have full overview of dens outside of this area. Patches of land at the outskirts of the study area, now characterized as of being of low risk are most likely influenced by the presence of red fox dens outside the study area, assuming that fox density is equal inside and outside the study area. This makes the chance of there being areas of refuge for roe deer fawns even more unlikely. Roe deer density had a negative effect on number of fawns observed per doe in autumn. This is in accordance with the observed density dependence in roe deer reproduction reported by Hewison *et al.* (1996) and Kjellander (2000). The effects of presence of lynx was not included in the best model, and this is somewhat surprising as lynx are known to kill about 12.5 % of a marked roe deer fawn population yearly at Grimsö Wildlife Research Area (II), but this effect was probably overridden by the effects of fox predation. Distance to the closest den was not included in the best model and this is possibly because of the generally weak and far reaching effects of fox dens in general.

Even if our result of weak, far reaching effects of fox dens depends on all parts of territories being used for hunting by red fox vixens or that the hunting along red fox territory boundaries is partially carried out by red fox

“floaters” or resident fox males, the fact remain, there are no refuges for roe deer fawns in the boreal forest.

3.4 The quality of mothers' home ranges and roe deer fawn survival (IV)

Maternal qualities may also affect offspring survival. Physical condition, age, experience, dominance rank, habitat choice and anti-predatory behavior are traits of a mother that is known to affect juvenile survival in different ways (Ozoga & Verme, 1986; Smith, 1987; Mech & McRoberts, 1990; Nixon & Etter, 1995; Byers, 1997; Nielsen *et al.*, 2004). In order to maximize their lifetime reproductive success females must balance their investment in their current offspring against investment in their own survival and their future reproduction (Stearns, 1997; Kjellander *et al.* 2004). This is referred to as a trade-off. In paper (III) we report on findings of such a female trade-off in roe deer does between good forage habitat and the predation risk for neonate roe deer fawns.

We investigated the relationships between predation risk of roe deer fawns and mothers' age, red fox density index and the size and habitat composition of the mothers' home range. In 1997-2004, 152 roe deer fawns were caught by hand and fitted with expanding VHF radio collars on the Bogesund study area. Seven of these fawns were not included in the study because of capture induced deaths, disappearance, and failed transmitters. The most common cause of mortality for red fox fawns in this study was red fox predation (88% of all deaths, other causes were hay mowing machines, starvation, hypothermia and disease) and in total 48% of the fawns died before the age of nine weeks. These results were similar to the generally observed pattern for northern temperate ungulates (Linnell *et al.*, 1995) and to previous Scandinavian roe deer studies. Predators, when present, cause the majority of neonatal deaths in roe deer (Aanes & Andersen, 1996; Jarnemo *et al.*, 2004; Jarnemo & Liberg, 2005, II).

In total, 94 adult roe deer does were followed for 277 reproductive events during the study period (1997-2004), and 46 of these does were of known age and with a determined home range, representing 109 reproductive events of known result. We found a strong positive correlation between mean yearly predation rate and fox index and between daily predation rate and a fox density index. We also found a significant positive correlation between female total home range size and area open habitat in does' home ranges with 10.0% of the variation in the area open habitat explained by total home range size. Furthermore, when we investigated the

combined effect of proportion open habitat in does' home ranges and fox density on the probability of females having one or more fawns, we found a significant negative effect of the interaction between the two variables "fox density" and "proportion open habitat", on the number of females with one or more fawns surviving the summer. A high predation risk in open habitats appears to be a common pattern in hider ungulate species (Beale & Smith, 1973; Carroll & Brown, 1977; Barret, 1981; Nelson & Wolf, 1987; Canon & Bryant, 1997) that have also been observed in roe deer (Aanes & Andersen, 1996; Panzacchi *et al.*, 2008). One reason for high predation rates in open habitats may be predators' opportunity to use the mothers as visual cues for locating neonates (Byers & Byers, 1983; FitzGibbon, 1993; Thompson, 1996). A patchy distribution of bed site cover in open habitat areas might also increase predation risk for hiding neonates compared to habitats where cover is more homogeneous (Beale & Smith, 1973; Autenrieth, 1980; Singer *et al.*, 1997). When facing risk of predation, animals have to balance food intake in rich, but risky habitats, against safety in a poorer habitat (McNamara & Houston, 1987; Lima & Dill, 1990). This evaluation of the landscape has been termed "the landscape of fear", defined as the spatial mapping of the predation cost of foraging (Laundré *et al.* 2001; Brown & Kotler, 2004).

Does that had a large proportion of open habitats in their home range had fewer surviving fawns in September than more forest-dwelling individuals in years of both high and low fox abundance, but if foxes had been lacking the outcome would have been quite the opposite (Figur 4).

Our study supports the suggestion by Aanes & Andersen (1996), that roe deer does who make use of open habitats get access to other valuable resources which may balance lower survival in neonates during summer.

The gains for roe deer females choosing these open risky habitats might not only be better survival of their fawns in years with low predation pressure, but also higher quality of surviving fawns and possibly, higher survival for themselves. We thus suggest that there is a trade-off between the gains and risks of using open habitats in roe deer does, and predict that the lifetime outcome of this high risk - high gain strategy might be as good as or possibly even better than that of choosing safer but poorer habitats.

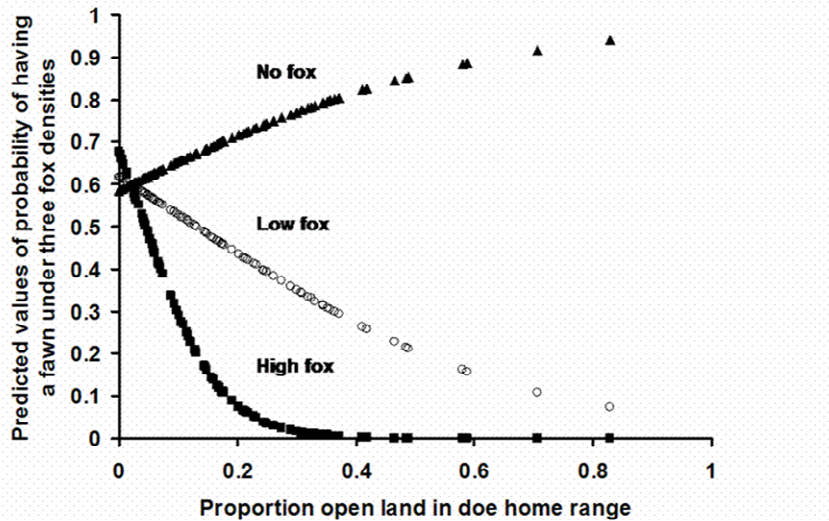


Figure 4. Probability for a female to have ≥ 1 fawn in September under three different fox densities as predicted from fox index and proportion open habitat in home range. The predicted values were calculated from a logistic regression model with data from Bogesund, Sweden, 1997–2003. No fox (black triangles) represents a model where fox index was set to 0, low fox (black circles) model includes the lowest observed fox index (0.1), whereas high fox (black squares) model includes the highest observed fox index (0.29).

3.5 Roe deer fawn survival and additional feeding of red foxes (V)

As we have seen red fox is considered a major predator of roe deer fawns (I; II) and red fox vixens with cubs are considered the largest threat to roe deer juveniles. The effects of red fox vixens' predation are reaching far from the dens, and there are simply put no refuges from red fox predation for roe deer fawns (IV). What then, are to be done by managers to minimize red fox predation on roe deer fawns? The simplest answer to this question is large scale culling of red fox vixens with dependant cubs, but this is not allowed in Sweden under current legislation.

We provided red fox vixens on Grimsö Wildlife Research Area additional food as close to active den sites as possible. The fox den survey revealed that 4 red fox litters were born at the research area in 2004 and

that 6 litters were born in 2005. Distances from fox dens with litters to feeding plots were on average 8433 m (990-12060 m) in 2004 and 5751 m (1056-6644 m) in 2005. The reasons for the relatively long mean distances between fox dens and feeding plots is explained by the way we designed the study. No fox den sites could be visited in advance as vixens are known to abandon den sites when disturbed by human presence, why feeding plots were placed out based on the most popular denning sites during the previous five years and the most used denning sites since 1973.

In 2004 bones or other remains from feeding plots were later found in one of the dens with litters in the northern area of supplemental feeding (distance between den and closest feeding plot 8321 meters) and in 2005 in two inhabited dens in the southern area of supplemental feeding (distances between dens and closest feeding plots 2111 and 1477 meters respectively). Red foxes visited all of the feeding sites frequently. We found no tracks or scats of wolves, lynx or wild boar at or near a feeding site.

Use of the additional food (percentage food removed) increased sharply at the beginning of feeding and reached a threshold level before or very early in the critical fawning period for roe deer. There was no relationship between number of fox visits and distance between fox dens and feeding plots and no overall difference in fawn per doe ratio among years during the study period. Supplemental feeding did not increase the fawn per doe ratio in autumn significantly when comparing years with supplemental feeding to years without supplemental feeding.

The best general linear model was the one containing year only and the second best model to explain variation in fawn per doe included distance between observed doe and feeding plot, and year. None of these models had a statistically significant effect on the number of fawns per doe and R^2 values were very low for all models.

It is always hard to establish negative results like these because they tend to depend on sample size which was marginal in our case. The measure of roe deer fawn survival may also be questioned because the best way to measure mortality in roe deer fawns is to monitor radio marked fawns directly. However, we failed to obtain sufficient sample sizes from radio marked fawns during these years. Fawn per doe ratio as recruitment measure cannot distinguish between fawn losses due to predation by other predators and fawn losses due to predation by red foxes, and as re-established lynx kill 12.5 % of radio marked roe deer fawns in our study area (II), this may partly mask effects of supplemental feeding of red fox.

Voles are supposedly main prey for red foxes at the study area and fluctuations in vole population density may influence fox predation on roe

deer fawns (Lindström, 1982; Kjellander & Nordström, 2003), but in spite of the fact that population density of voles was low in 2004 (0.25 voles /100 trap nights) and high in 2005 (1.51 voles / 100 trap nights), there was no significant differences in fawn per doe ratio between the two years. This result may be interpreted as a support for effects of supplemental feeding, as differences in predation pressure on roe deer fawns between years of high and low vole population densities might have been leveled out by supplemental feeding, but mean fawn per doe ratio was actually lower in 2005 (0.85 fawns per doe), than in 2004 (1.47 fawns per doe), indicating a negative relationship between vole density and number of fawns per doe.

However, this is the actual situation that management is facing, so our main result that additional feeding of red fox during the roe deer fawning season do not increase overall roe deer recruitment is likely valid in the current multi-predator situation of boreal Sweden. The low density of roe deer in the area makes it possible that red fox is not actively searching for roe deer fawns because it is a fairly rare prey item. Red fox predation on fawns at the Grimsö Wildlife Research Area amounts to about 17 % of radio marked fawns (II) which is much lower than compared to that reported from more agricultural areas (Aanes & Andersen, 1996 (50%); Jarnemo & Liberg, 2005 (42 %)) where foxes also can act as roe deer fawn specialists during early summer (Panzacchi *et al.*, 2008).

This low predation rate within Grimsö Wildlife Research Area is most likely related to low population densities of both red fox and roe deer, as well as landscape structure. This situation is likely to be representative for large parts of the boreal forest in Scandinavia. For this reason we suggest that red fox predation on roe deer fawns in boreal forest might be purely incidental (Vickery *et al.*, 1992) in which case predation may occur, at a low level, even if red fox is provided with supplemental food.

Nevertheless, the negative result holds only for the scale we choose as relevant and for the level of red fox predation common to our area. Thus, results from this study clearly suggest that supplemental feeding of red foxes will most likely not be a solution to this management issue or an alternative to predator removal. However, in agriculturally dominated areas where roe deer density and red fox predation rates are higher, and where foxes may act as specialist predators on roe deer fawns (Panzacchi *et al.*, 2008) we cannot exclude that supplementary feeding may increase roe deer recruitment, especially if lynx predation is low.

4 Future perspectives

By revealing the past it is almost impossible to avoid predicting the future as we, most probably, already are beginning to see the consequences of a major change in the basis for boreal species dynamics; the climate. If vole dynamics in South-central Sweden are affected by milder winters then it is here that we see the effects first of what is to come later further north. The disruption of fully functioning predator-prey systems may have detrimental consequences that are hard to predict in the long run. Generalist predators like the red fox can always manage by prey switching if vole population lows become permanent, but all predators are not that plastic in their nutritional needs and behavioral traits. Specialists like certain owls, weasels and stouts may suffer hard from constant lows in the vole cycles making their population densities lower and making them more vulnerable to local extinction and other stochastic events. Will the northern system be replaced by the southern or will we see the emergence of totally new dynamics in the boreal forest? Will indeed the boreal biome survive at all with rising temperatures and less snow cover? Future research should, in my opinion, focus on finding the mechanisms that link global warming to population dynamics.

The roe deer population development in Sweden has been a true success story during the 20th century, but now the trend has turned. Local roe deer population densities in Sweden will most likely become even more depressed from predation by red fox, lynx and wolves in the future as lynx and wolves continue to spread further south. On the other hand climate change in the form of global warming will probably make winters warmer and that will be beneficial for survival. Another species re-introduced and re-colonizing Sweden is the wild boar. This species is now spreading at tremendous speed all over the country. How this will affect roe deer is yet unknown, but future studies should be focusing on direct or indirect

competition effects between the species. Roe deer is not only a species important for predators, but is widely recognized as one of Sweden's most important game species. Nevertheless, managers in general have not seen roe deer as a species important to manage, because of its abundance. In these days of decreasing population densities and dwindling hunting bags it might be about time to start managing roe deer more actively. Perhaps it is time to develop new and updated harvest models including different scenarios with and without snow, with lynx but no wolf, no lynx but with wolf, with both lynx and wolf etcetera. For this purpose we should use robust models based on simple density estimates or proxies for density and bag size and all the other parameters needed. Long term studies and applied experimental approaches to roe deer research will be necessary to provide proxies and evaluate management strategies.

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