The ecology of red fox predation on roe deer fawns with respect to population density, habitat and alternative prey

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Doctoral Thesis

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APPENDIX - LIST OF MANUSCRIPTS

The present thesis is based on five manuscripts, which are going to be published in scientific journals. In this Ph.D. thesis, they will be referred to by their Roman numerals. Follows a list of titles:

I. *When a generalist becomes a specialist: patterns of red fox predation on roe deer fawns under contrasting conditions.*

Panzacchi M., Linnell J.D.C., Odden J., Odden M. & R. Andersen

II. *Family effects and multi-scale consequences of landscape composition on roe deer fawns' predation risk to red foxes.*

Panzacchi M., Linnell J.D.C., Odden M., Odden J. & R. Andersen

III. *Evaluation of the importance of roe deer fawns in the spring-summer diet of red foxes in south-eastern Norway.*

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IV. *Effect of land-use on small mammal abundance and diversity in a forest-farmland mosaic landscape in south eastern Norway.*

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Panzacchi M., Herfindal I., Linnell J.D.C., Odden M., Odden J. & R. Andersen

INTRODUCTION

In an era when agriculture, commercial forestry and human settlements occupy as much as 95% of the terrestrial environment (Western & Pearl 1989), and the resulting loss of biodiversity is one of the major issues humankind has ever faced (Pimentel et al. 1992), some species defy the general trend and thrive throughout most of their range. The ecological success of those species is related to their adaptability to different ecological conditions, as it is reflected by the wideness of their distribution.

Perfect examples of successful wild mammals in the human-dominated temperate zone of Eurasia are the red fox (*Vulpes vulpes*), the roe deer (*Capreolus capreolus*), and small rodents (mice and voles). These species occur in most natural, semi-natural, and moderately artificial habitats available within their distribution range, which, in Europe, extends from Portugal to Russia, and from Mediterranean countries to northern Scandinavia. Within the human-modified landscape characterising their overlapping ranges, these species have developed a wide range of ecological interactions, including predator-prey relationships.

The red fox has long been known as the archetypal opportunistic omnivore feeding on virtually every type of animal and plant food according to availability. However, ever since the first studies on red fox diet it has been clear that small mammals were the preferred prey item in the majority of ecosystems (Lindström et al. 1994). Larger prey such as the roe deer were detected in the predators' scats, but were suspected to be mostly scavenged as carcasses, and not actively preyed upon (Lund 1962 and references therein). Deeper investigations of the topic were prevented by the elusive behaviour of roe deer and, in particular, of their fawns – the most likely age class susceptible to predation from the medium-sized predator.

The introduction of radio-telemetry techniques in the 1960's (Cochran et al. 1963) has revolutionised wildlife research and provided the opportunity to obtain precise, individual-based, data on the behaviour, mortality and population dynamics of a variety of species. Radio-telemetry studies have revealed that the undisputed major predator for roe deer fawns is the red fox, and that the annual predation can be as high as 90% (Jarnemo & Liberg 2005). However, temporal and spatial variation in neonatal predation rates and patterns remain significant and, due to the limited number of long-term comparative studies on juvenile mortality, virtually unexplored.

In spite of half a century of research on predator-prey relationships on both theoretical and empirical ground, the complexity of factors affecting this interaction have not been fully understood. In order to contribute to the debate regarding factors affecting predator-prey interactions we provide data from the red fox - roe deer fawn – small mammal system in a highly modified landscape in south eastern Norway.

THEORETICAL BACKGROUND

Large herbivore population dynamics are commonly characterised by constant adult survival and variable juvenile recruitment (Gaillard et al. 1998a). As a result, variation in population growth rates is primarily driven by changes in neonatal mortality, which is the most fluctuating and unpredictable among demographic parameters (Gaillard et al. 1998b; 2000). A great deal of the variability in juvenile survival among study areas is accounted for by the mere presence or absence of predators. A literature review revealed that, in areas inhabited by predators, neonatal mortality of temperate ungulates average 50% of the production, versus 20% in predator-free areas, and that predation is by far the most frequent cause of death being responsible for about 70% of the losses (Linnell et al 1995).

In the case of roe deer, the most important predator for the newborn fawns throughout the range is the red fox (Lindström et al. 1994; Wotschikowsky & Shwab 1994; Aanes & Andersen 1996; Jarnemo & Liberg 2005). Hence, where present red foxes have the potential to be one of the major determinants of roe deer population dynamics, and an increasing amount of evidence supports the hypothesis that in populations not subjected to density dependent effects on fawn survival red fox predation can be additive (Jarnemo 2004a, Lindström et al. 1994). Still, temporal and spatial variation in neonatal predation rates and patterns remain significant and, due to the absence of adequate data, *i.e.* from long-term comparative studies on individually marked animals (Gaillard et al. 2000), in particular in areas inhabited by predators, virtually unexplored.

FUNCTIONAL RESPONSE

A predator's functional response describes how consumption rates of individual consumers vary with respect to resource density, before reaching a plateau due to saturation processes (Solomon 1949). Holling (1959) described three types of functional responses: *Type I* (*linear*; the predator's consumption rate is proportional to prey density; rare in nature); *Type II* (*cyrtoid*; the predator's consumption rate increases at a decreasing rate with prey density until it becomes constant at satiation; typical of specialist predators); *Type III* (*sigmoid*; the predator's consumption rate is low up to a certain threshold in prey density, and then rapidly increases following the so-called prey-switching behaviour; typical of generalist predators).

The predator's functional response has been theoretically recognised as a major factor determining the impact of predation on prey populations. However, there is still a remarkable scarcity of publications investigating factors affecting predator consumption rates under free-ranging conditions (Abrams & Ginzburg 2000; Miller et al. 2006). This is mostly due to the difficulties associated with the calculation of a functional response for wild species, which requires long-term studies on radio-monitored individuals with a good knowledge of the density of predators, the density of main prey, the density of alternative prey, predation rates, the habitat structure, and behavioural parameters.

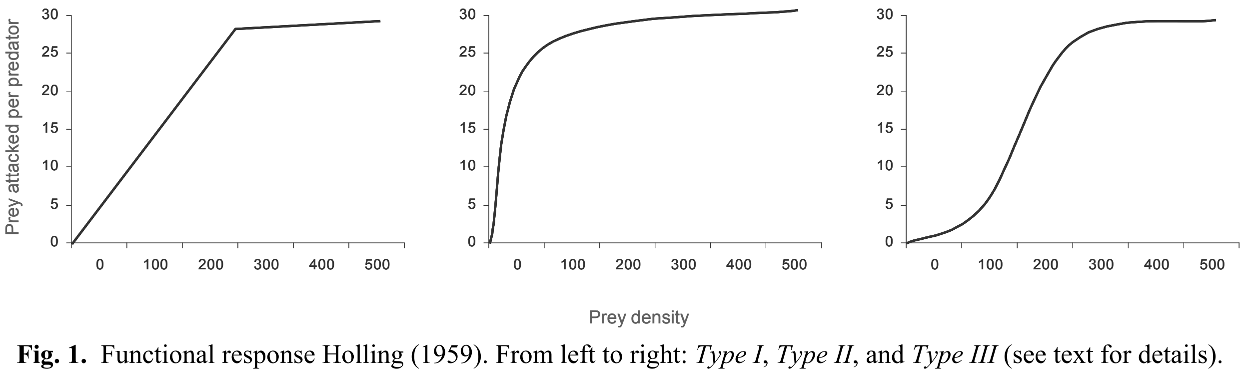

Fig. 1. Functional response Holling (1959). From left to right: *Type I*, *Type II*, and *Type III* (see text for details).

Factors Affecting the Functional Response

Population processes are intrinsically discrete, and population dynamics are shaped by the combination of the behavioural decisions of each individual. Indeed, long-term studies on radio-marked individuals have revealed that, for a given ecological setting, individual variation can lead to remarkable variation in fitness components at the population level (Gaillard et al., 2000). Thus, the starting point for the understanding of predator-prey interactions at the population level is the investigation of factors affecting individual behavioural decisions.

According to Endler (1986), a predator-prey interaction can be subdivided into the following steps: encounter, detection, identification, approach, subjugation and consumption. All of these steps are affected first of all by the probability that the predator-prey encounters occur and this, in turn, depends mostly on population **density**. **Habitat** composition has the potential to affect population densities of both predators and prey and, thus, alter predator-prey encounter probabilities and predation risk. In addition, habitat heterogeneity - *i.e.* the presence of preferred habitat types - and prey **behaviour** and anti-predator behaviour are confounding variable which have the potential to virtually alter the “real” population density - the one perceived by the animals - and thus the probability of predator-prey encounters. Finally, the abundance and distribution of **alternative prey** may alter the both the profitability of the main prey (*i.e.* the energetic convenience, from a predator’s point of view, in hunting for a specific prey item instead of another) and the predators’ searching behaviour, with potential effects on the functional response and on predation rates.

The Red Fox - Roe Deer - Small Rodent System and the Alternative Prey Hypothesis

The understanding of factors affecting variation in neonatal predation rates and patterns requires long-term data on radio-monitored individuals and, thus, only recently an increasing number of articles started exploring this topic (see Gustine et al. 2006, for a review of north American studies; Owen-Smith et al. 2005). In the case of roe deer and red foxes, the available information comes for the most part from studies conducted in Scandinavia (Aanes & Andersen 1996; Linnell et al. 1995; Jarnemo 2004a), which confirmed the role of red foxes as the most important predator for the newborn ungulates. Indeed, temporal variation in the abundance of red foxes has been recognised as a major factor in determining roe deer fawn survival rates (Jarnemo & Liberg 2005). However, the conclusions regarding the impact of predation with respect to roe deer fawns’ age, sex, growth rates, and birth date have not always been consistent. On the contrary, all these studies indicated a higher risk of predation in open areas as compared to forests, as the neonatal hiding strategy (Lent 1974) developed in order to limit predation in the presence of cover. However, the direct mechanisms through which this happens were investigated only recently, while the indirect effects of habitat characteristics on predation risk (*e.g.* through altered movement patterns, growth rates, and spatial distribution of predators, prey and alternative prey) remain largely unknown.

The Alternative Prey Hypothesis (APH) states that a generalist predator switches from one prey to another as the profitability of the latter increases with respect to the former (Lack 1954). One prediction from the APH states that a medium-sized predator, commonly feeding upon small-sized prey, switches to juveniles of large alternative prey species as they become available once a year (Hörnfeldt 1978). This hypothesis has been validated in the red fox - small rodents - roe deer fawns system by a 28-years study in south-central Sweden (Kjellander & Nordström 2003). The study showed that annual survival rates of roe deer fawns were positively correlated with the abundance of small rodents, which was subjected to multi-annual fluctuations, and negatively correlated with the number of fox litters in the previous year. Thus, the study fully supported the APH for the red fox - small rodents - roe deer fawns system, and suggested that temporal fluctuations in the abundance of the red fox's main prey affects predation rates on the alternative one.

AIMS OF THE Ph.D.

The main aim of the Ph.D. was to investigate factors responsible for variation in red fox predation rates and patterns on roe deer fawns, with particular attention to **population density**, **environmental variables, behavioural parameters**, and **alternative prey**.

In particular, by analysing 8 years of data on radio-monitored roe deer fawns we investigated the impact of red fox predation in a wide area in south-eastern Norway characterised by a gradient in predator and prey density and in habitat characteristics. The southern part of the study area was very productive and fragmented, with a high percentage of agricultural land and medium-high roe deer and red fox densities. The northern study area was dominated by dry boreal forest with only a few, small, cultivated fields, and was characterised by a 26-times lower prey density. These ecological settings were optimal in order to test hypotheses on the effect of population density, habitat characteristics and habitat-related behavioural parameters on roe deer fawns' predation risk. The influence of population density on predation risk has been thoroughly investigated in *Manuscript I* and *Manuscript II*, while the influence of behavioural parameters and habitat characteristics at the landscape scale and at smaller spatial scale has been investigated in *Manuscript II* and *Manuscript V*, respectively.

In addition, we focused on the effect of the spatial distribution of red foxes' main prey (*i.e.* small rodents) on roe deer fawns' predation risk. Hence, at first we conducted a two-year study on the feeding habits of red foxes in order to assess the relative importance of roe deer fawns and small rodents in the diet (*Manuscript III*). Also, we conducted a two-year study on the abundance and distribution of several small rodents' species in different habitat types (*Manuscript IV*). The conclusions of all these studies provided the basis for testing hypothesis regarding a higher predation rate for fawns hiding more often in habitat types characterised by a higher abundance of red foxes' preferred prey (*Manuscript V*).

STUDY AREA

The study was conducted in south-eastern Norway. Roe deer fawns were studied from 1995 to 1998 in Hedmark County, hereafter referred to as the northern part of the study area, and from 2001 to 2004 in the neighbouring Counties of Østfold and Akershus, referred to as the southern part of the study area. The study area encompasses a gradient in latitude, climatic conditions and habitat structure and composition. In the northern part of the study area 88% of the landscape is covered by coniferous forests and bogs, 9% by water, and only 3% by cultivated fields; the climate is continental with cold, snowy winters and warm summers. On the contrary, the southern part of the study area is made up of a fine mosaic of agricultural areas (24%), water (11%) and forests (65%), both coniferous and deciduous; the climate is milder and the snow cover is less persistent compared to the northern area. *Manuscripts I* and *II* refer to the overall study area, while the others refer only to the southern part of the study area. The main predators for roe deer in the study area are Eurasian lynx (*Lynx lynx*), wolves (*Canis lupus*), red foxes, and human hunters.

MATERIALS AND METHODS

ROE DEER FAWNS

A total of 153 roe deer fawns (55 in the northern area, 98 in the southern area) were captured soon after birth and provided with expansible radio-collars. The fawns were captured by stalking radio-collared does or other lactating mothers. When only one fawn was captured, we searched the area surrounding it in order to find the siblings; in total, we captured individuals belonging to 83 different family groups. All fawns were weighted at capture and in 61 cases they were re-weighed on average after 6 days in order to measure their daily growth rate. Due to collar failure, we lost contact with two of the captured fawns, which were excluded from mortality analyses. Every fawn was radio-monitored approximately every day for the first two months of life in order to record daily movements and mortality causes. Both coarse-scale habitat types (meadow, clear-cut, crop, young forest and mature forest) and fine-scale vegetation descriptors (percentage cover and average height of herbaceous plants, moss, berries, bushes and branches) were recorded within a 15 x 15 m quadrate centred within each roe deer fawn's bed site. In addition, indices of visibility were recorded for both the roe deer fawns and mother. Causes of death were assessed directly in the field or, in uncertain cases, at the Norwegian Veterinary Institute, Oslo.

RED FOX

We conducted a study of red fox diet in Østfold and Akershus Counties during May-August 2003 and 2004. A total of 171 fox scats were collected, stored in plastic bags and frozen at –20°C. Of these, 147 scats were collected by walking 6 transects (1 to 6 km long) previously cleaned from old scats, and while carrying out routine radio tracking of roe deer and red foxes (thanks to a parallel study on the ecology of the red fox ongoing in the study area). In addition, we visited two dens within the study area and we collected 24 scats representative of the spring-summer diet of red fox cubs. Only fresh scats were collected. Scats analysis was performed by following the methods suggested by Putman (1984), Reynolds & Aebischer (1991). The discrimination among different taxa of medium-large mammals (different species of ungulates, mustelids, insectivores and domestic animals) was done by a microscopic hair analysis of the cuticle, section and medulla using a 400 X microscope. Different species of small mammals were identified through the microscopic analysis of jaws and teeth. The red fox diet was assessed by using the Frequency of Occurrence (FO, Leckie et al. 1998) and the Whole Scat Equivalent method (WSE; Angerbjörn et al. 1999) based on the Estimated Ingested Volume (EIV, Kruuk & Parish 1981).

INDICES OF ROE DEER AND RED FOX ABUNDANCE

We obtained indices of red fox and roe deer abundance thanks to annual wildlife censuses carried out in southeastern Norway by the Norwegian Association of Hunters and Anglers (Hedmark, Østfold and Akershus county offices), the Office of Environmental Affairs in Hedmark County, Hedmark University College and the Norwegian Institute for Nature Research since 1995. The censuses were conducted by snow tracking along standard transects and recording the number of roe deer and red fox tracks crossing the transects. In total, 880 km were skied in Hedmark and 240 km in Østfold and Akershus Counties. The indices of abundance were expressed as number of tracks km-1 24 hrs-1, corrected for the number of days after the last snowfall. By using digitised maps we have been able to investigate the relationship between the indices of abundance of roe deer and red fox and the structure and composition of the landscape surrounding the transects at different spatial scales (*Manuscript II*).

SMALL MAMMALS

We conducted a capture-mark-recapture study on a non-cyclic population of small mammals in Østfold and Akershus Counties. Small mammals were trapped during May-August 2003 and 2004 using baited Ugglan Special multi-capture live-traps (Hansson 1994), designed for capturing shrews, mice and voles. Each individual (apart from shrews) was marked by clipping a small spot of fur on its back before being released. Small mammals were trapped each year during 5 trapping sessions lasting 10 consecutive days each, for a total of 100 trapping days in two years. The traps were organised in Small Quadrates (SQs, Myllmäki et al. 1971), which are 15 x 15 m trapping units composed of 12 traps evenly positioned along the perimeter. The SQs were distributed in six habitat types, as described for roe deer fawns. We adopted a similar study design for roe deer fawns and for small mammals in order to obtain comparable data. Hence, within the perimeter of each SQ we recorded several vegetation parameters, by following the same procedure adopted when recording environmental variables within the 15 x 15 m quadrate surrounding each roe deer fawn’s bed site. All traps were checked every morning for 10 consecutive days, and then moved to another area.

STATISTICAL ANALYSES

Statistical analyses were conducted using R version 2.4.0 for windows (R Development Core Team 2006), and SPSS statistical software for Windows, version 12.0. Landscape analyses were conducted on digitised forestry maps by using the software ArcView GIS 3.2. Capture-mark-recapture analyses on small mammals were performed with MARK 4.3 (White & Burnham 1999), and species richness and evenness were estimated by using Ecosim 7.69 (Gotelli & Entsminger 2006).

RESULTS AND DISCUSSION

ROE DEER FAWN MORTALITY *(Manuscript I)*

From birth to the 25th of September, the beginning of the hunting season for roe deer family groups, 34% of the captured fawns died (Table 1). In the southern study area mortality was more than two times higher than in the northern one. Predation was the major cause of death, and the role of red fox as the main predator for roe deer fawns was confirmed (Aanes & Andersen 1996; Jarnemo 2004a), since it was responsible for 62% of the losses. While in the southern study area foxes killed one out of 4 fawns, in the northern area only one fawn out of 8 was preyed upon. Sex ratio was even at capture and did not affect predation risk, which occurred on average at 23 ± 14 days (St.d.). Hay-mowing machines were the second cause of mortality, while predation by lynx and dogs, or other causes of death were of minor importance.

Table 1. Mortality of roe deer fawns in the northern and southern study areas during 1995-98 and 2001-4, respectively.

Study area	Mortality causes (N of fawns dead)								Mortality, % *	Fox predation rate, % †	Mortality due to fox % ‡
	Predation			Mower	Accident	Stillbirth	Disease	Not known			
	Fox	Lynx	Dog								
Southern	21	3	1	7	1	2	1	4	41.67	25.30	58.33
Northern	7	1	0	0	1	0	0	2	20.00	13.21	77.78
TOT	28	4	1	7	1	2	1	7	33.77	20.59	62.22

* Percentage of fawns that died

† Percentage of radio-marked fawns with known fate killed by fox; excluded fawns killed by mowers

‡ Percentage of known mortality causes due to fox predation

IMPORTANCE OF ROE DEER FAWNS TO THE DIET OF RED FOXES (*Manuscript III)*

Even though red foxes are the major predator of roe deer fawns throughout their range and have the potential to severely affect roe deer population dynamics, it is unclear to what extent the newborn ungulates constitute an important part of the diet of the predators. Hence, parallel to the study of roe deer fawns' predation risk, we analysed the feeding habits of adult red foxes and of their cubs during spring and summer in the southern part of the study area.

Even though the overall diet of red foxes was highly varied, the study showed that small mammals constituted the most important food item, accounting for 33% of the overall volume ingested (Fig. 2); among these, the field vole *Microtus agrestis* was the preferred species. Medium-large mammals were the second major component of the diet (25% volume) and, among these, roe deer largely predominated (34%). Similar results were obtained by O'Mahony et al. (1999). The category "invertebrates" had the highest frequency of occurrence (FO) and was recorded in approximately one fourth of the scats.

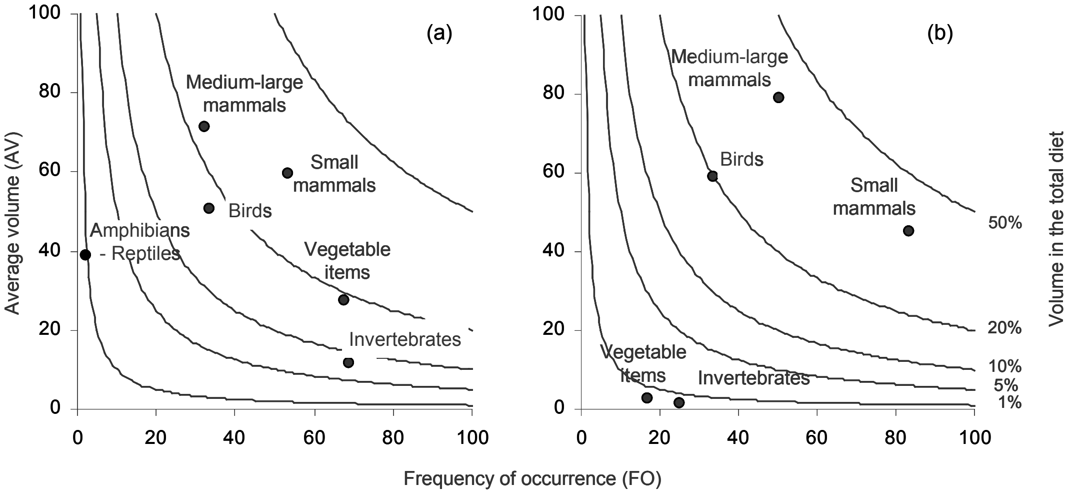

Fig. 2. Representation of the diet of adult red foxes (a) and cubs (b) in south-eastern Norway during May-August 2003 and 2004. Each figure illustrates the relationship between the frequency of occurrence (FO) and the average volume (AV) of the main food items. The isopleths indicate the relative volume of the considered food item with respect to the total volume of all food items. *E.g.*: in (b) the birds occur in 33 % of the scats and account for 60 % of the volume of each of those scats; they represent about 20 % of the volume in the overall spring-summer diet of red fox cubs.

The analysis of temporal variation in the diet composition of adult foxes showed that the FO of small rodents did not increase as their seasonal increase in availability but, on the contrary, significantly decreased with time (Fig. 3b). The importance of roe deer in the diet of adult red foxes was highest in early spring (Fig. 3a), thus supporting previous findings (*Manuscript I*) indicating that, in this study area, the predator started actively hunting for the newborn ungulates from the very beginning of the birth season. Hence, as summer progressed adult foxes included a higher proportion of invertebrates and vegetable items (for the most part berries) in the diet, which, during summer, turned out to be more diverse than expected at these northern latitudes.

On the contrary, the diet of cubs not so diverse, and included a much higher proportion of large prey (*i.e.* small mammals, medium-large mammals and birds) compared to adults. In particular, roe deer remains occurred more frequently in scats found at dens (25%) compared to scats from adult foxes (9 %), indicating that vixens were using fawns to feed their cubs. Similar conclusions were suggested by Lindström (1994).

Hence, our results confirm the predominant role of small rodents, and in particular of *M. agrestis*, as preferred food item for the red fox in northern ecosystems (Lindström 1982; O'Mahony et al. 1999). However, adult foxes killed roe deer fawns as soon as they became available during early spring (see also *Manuscript I*). As the season progressed and fox cubs started eating solid food, larger prey item were carried to the dens, while adult foxes relied upon other smaller and more easily accessible food sources such as berries and insects.

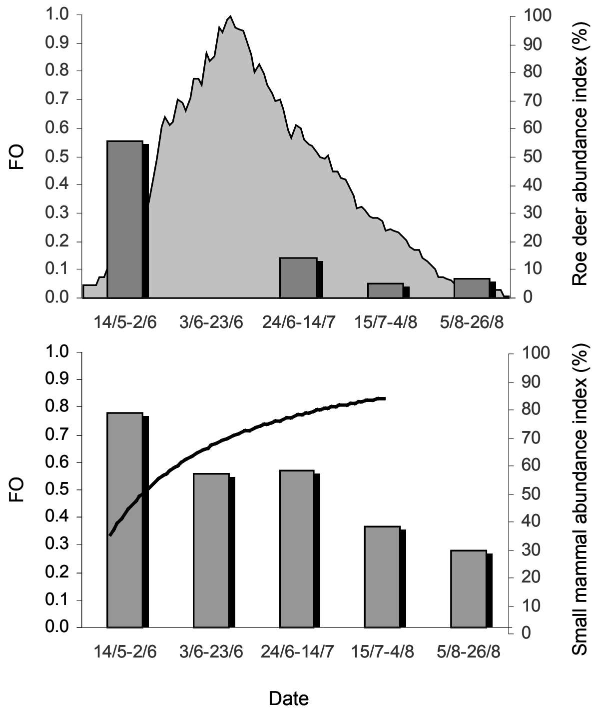

Fig. 3. (a) Frequency of occurrence of roe deer fawns (bars) compared to the index of abundance of roe deer fawns (shaded area) in the stage when they are vulnerable to red fox predation. (b) Frequency of occurrence of small mammals (bars) compared to the index of abundance small mammals (curve) calculated from the 21st of May to the 2nd of August 2003 and 2004. The indices of abundance are expressed as percentages with respect to the maximum values calculated during spring and summer. Both the index of abundance and the FO of small mammals refer to: *Microtus* spp., *Chletrionomys* spp., *Apodemus* spp. The indices of abundance of small mammals and of roe deer fawns refer to the same study area where the red fox scats collection has been carried out.

We suggest that in some situations roe deer fawns can constitute a relevant food source for red fox cubs (see also Lindström 1994). However a long-term study in southern Sweden showed that when the population density of voles, which was subjected to marked multi-annual fluctuations, was higher, mortality of roe deer fawns was minimal and vice-versa (Kjellander & Nordström 2003). This suggest that roe deer fawns can represent a key resource whenever their net profitability exceeds that of the main prey item - as it can happen in areas where small rodent populations are cyclic -, or of other alternative large prey items (*i.e.* birds, hares, domestic animals).

We suggest that in our study area the medium-high density of roe deer, which enhanced the profitability of hunting fawns, induced the predator to use roe deer fawns as one of the main prey items for raising the cubs. However, considering the wide food spectrum and the availability of several large prey items in our study area, we suggest that roe deer fawns are not an irreplaceable food item, and it appears unlikely that the importance of fawns to the diet of foxes, and hence on their population dynamics could be as great as the impact that the predator has on roe deer populations.

PREDATION RISK *vs.* RED FOX FUNCTIONAL RESPONSE (*Manuscript I*)

By using the predator's consumption rates and an index of roe deer fawns' "exposure", indicating the daily availability of radio-monitored roe deer fawns belonging to the age classes preferred by fox (Fig. 4, shaded areas), we explored the red fox functional response in the two study areas. The shape of the functional response varied significantly between the two study areas (Fig. 4), and we suggest that this difference reflected differences in prey profitability, *i.e.* in the energetic convenience, from the red fox point of view, in hunting for roe deer fawns instead of for searching for other prey items.

The profitability of a given prey item increases first of all with its abundance, parallel with the predator-prey encounter rate. Hence, roe deer fawns' profitability should be considerably higher in the southern study area compared to the northern. Moreover, profitability can be affected by habitat characteristics. Since the hiding strategy adopted by roe deer fawns evolved in order to limit predation risk in presence of cover (Linnell 1994; Lent 1974), newborn ungulates tend to be more vulnerable to red fox predation when selecting open, agricultural areas compared to woodlands (Aanes & Andersen 1996; Jarnemo 2004a; Jarnemo et al. 2004 b). Hence, roe deer fawns' profitability should be further enhanced in the southern, agricultural study area.

According to our expectations, in the southern area the high fawn profitability induced a red fox consumption rate closer to the specialist end in the specialist-generalist continuum of feeding habits. Conversely, the low fawns' profitability in the northern forest-dominated area characterised by low prey density promoted a *Type-III* functional response typical of archetypal generalist predators. Thus, our results support the conclusions of Krivan & Eisner (2003) and Prugh (2005), which rejected a strict dichotomy between specialist and generalist predators and suggest that a single species can adjust foraging strategy in relation to prey profitability in different ecological settings.

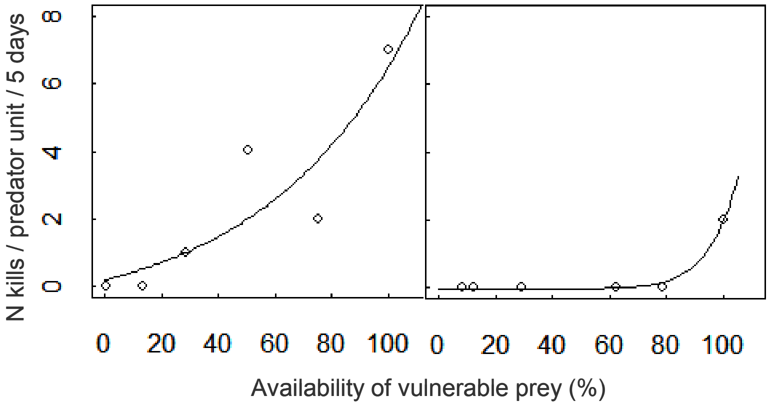

Fig. 4. Consumption rate of the red fox populations inhabiting the southern (Østfold-Akershus, left) and northern (Hedmark, right) study areas during the increasing phase of the availability function of roe deer fawns in the vulnerable stage, which occurred during a 35 days period

The different functional responses were responsible for the observed different rates and patterns of predation. In our study area, 80% of roe deer fawns were born between the 27th of May and the 19th of June, and the birth period did not differ among years or study areas. In the southern area foxes started actively hunting for the newborn ungulates from the very beginning of the birth season, and caused a higher predation risk for fawns born before or at the beginning of the birth peak (Fig. 5). Given the limited time during which fawns are vulnerable to red fox predation, this resulted in an overall higher impact on neonatal mortality rates (25%). On the contrary, in the northern study area fawns were killed for the most part when they were encountered opportunistically during the peak in prey availability; thus, fawns born at the beginning of the birth season were relatively safe, and the overall predation rate was lower (13%).

The flexibility of the functional response may help explaining the contrasting results found by previous studies (Aanes & Andersen 1996; Jarnemo et al. 2004 a) regarding the impact of predation with respect to birth synchrony. Moreover, our findings show that the selection pressure from red fox predation can act either towards or against a synchronous birth season in roe deer and, consequently, support the hypothesis that reproductive synchrony in roe deer evolved primarily in response to habitat seasonality and not, as previously hypothesised, as an anti-predator strategy.

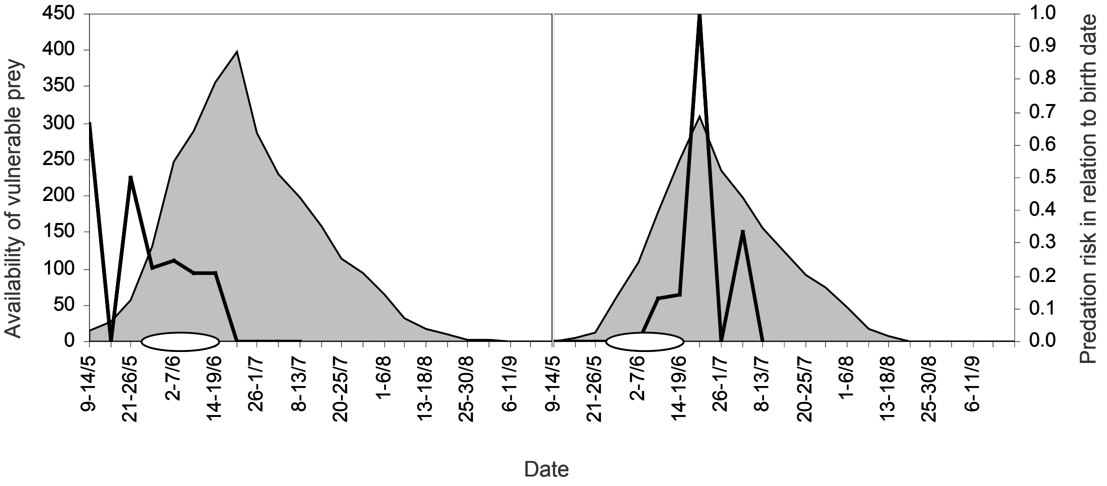

Fig. 5. Red fox predation risk (line) in relation to birth date and to the index of roe deer fawn availability in the southern (Østfold-Akershus, left) and northern (Hedmark, right) study areas. The index of availability (shaded area) was calculated as the number of fawns alive in each time interval, belonging to the age classes vulnerable to fox predation. The ellipses show the birth peak, *i.e.,* the period during which 80% of the births occurred.

PREDATION RISK *vs.* LANDSCAPE CHARACTERISTICS (*Manuscript II*)

Wide-scale landscape structure and composition may influence red fox predation risk directly, by altering the overall roe deer detectability (*Manuscript V;* Jarnemo 2004b), and indirectly, by altering prey and predator densities, roe deer movement patterns, and fawns' growth rates (Fig. 6). These hypotheses have been tested by adopting a multi-scale approach. At first, we investigated the relationship between the indices of abundance of roe deer and red fox and landscape characteristics within regions, municipalities, and buffers with different radii (5 km and 2.5 km) built around each transect used for assessing the above-mentioned indices of abundance. After, we adopted a similar multi-scale approach and investigated the relationship between roe deer fawn predation risk and landscape structure and composition within regions, municipalities, and buffers with different radii (5 km, 2.5 km, and the average radius of a spring-summer home range) built around the activity centre of each family group (Fig. 7).

At most spatial scales, forest fragmentation by agricultural land negatively affected roe deer mobility and positively affected the indices of abundance of both roe deer and red fox. The most parsimonious logistic regression model explaining predation risk with family group as random variable and the above-mentioned landscape descriptors, movements and indices of abundance of roe deer and red fox as explanatory variable, indicated that the likelihood of a fawn being killed by a fox increased with the proportion of agricultural land within the 2.5 km buffer, with roe deer abundance, and with shorter movements.

We suggest that effect of fragmented agricultural areas on predation risk is related to several factors operating at different spatial scales. Roe deer abundance and activity increased in the ecotone belt, thus enhancing predator-prey encounter rates and, consequently, predation risk (see *Manuscript I*). Moreover, we evidenced an increase in red fox activity patterns with habitat fragmentation, which is likely to be due to the higher abundance of roe deer (see also Bunnefeld et al. 2006), and also to the higher abundance of other prey items commonly associated with ecotones (Andrén 1995; Andrén & Agelstam 1988).

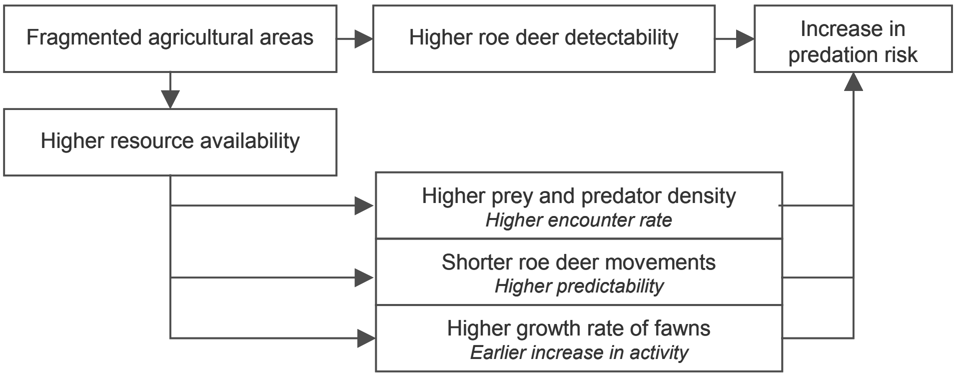

Fig. 6. Block diagram illustrating the hypotheses discussed in this paragraph regarding factors affecting the probability of a roe deer fawn of being killed by a red fox. Suggested reasons underlying the hypotheses in italic.

Habitat structure and composition markedly affected roe deer movements which, in the southern, more productive study area, were half the size compared to the northern area. Movements, in turn, affected predation risk, with shorter movements enhancing prey predictability and, thus, predation risk. However, this pattern was much more evident in the northern study area compared to the southern. The northern area is characterised by a widely homogeneous, forest-dominated landscape with very few, small cultivated fields. Thus, we suggest that in the northern study area restricted movements in proximity of small cultivated fields remarkably enhanced roe deer spatial predictability and, thus, predation risk.

However, we hypothesise that, depending on the landscape structure and composition, on predators and prey density, on their patterns of resource utilisation, and on the predator's functional response, movements may either enhance predation risk by increasing the probability of predator-prey encounters (Ozoga & Verme 1986) or, on the contrary, decrease it by reducing prey predictability (Mitchell & Lima 2002).

In contrast with previous studies (Pettorelli et al. 2001), we found no relationship between landscape characteristics, roe deer fawn growth rate, and predation risk. The fact that fox-killed fawns had the same body mass as surviving individuals has been also documented by Aanes & Andersen (1996), and indirectly supports the hypothesis that red fox predation on roe deer fawns is additive (Lindström et al. 1994; Jarnemo et al. 2004b).

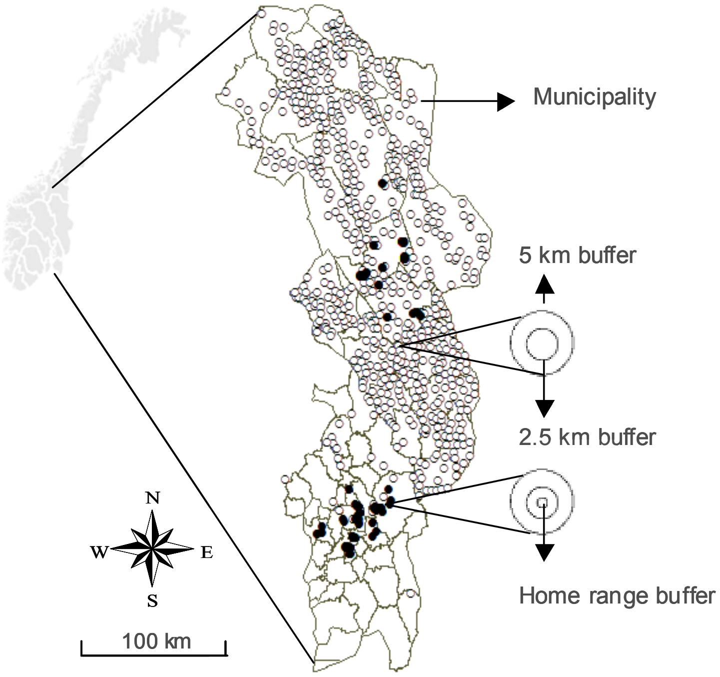

Fig. 7. Location of the study area in south-eastern Norway (left), encompassing Hedmark, Østfold and Akershus counties (respectively, from north to south), and study design (right). Each dark dot represents the centre of activity of a radio-monitored roe deer family group; circles indicate the location of transects used for estimating the indices of abundance of red fox and roe deer. The study was carried out by adopting a multi-scale approach, and landscape characteristics were investigated in the area surrounding each roe deer family group and each transect at the Municipality scale, and within buffers with a radius equal to 5 km, 2.5 km, and within a home-range buffer.

"FAMILY EFFECTS" IN PREDATION RISK *(Manuscript II)*

Given the strict association between siblings during the first months of life, we hypothesised that relatedness among siblings (*i.e.* family effects; *sensu* Gaillard et al. 1998b) would affect predation risk. By analysing data referring to 43 different family groups, our results demonstrate that after a fox killed one member of a family group, the probability of a sibling being killed rose from 20% up to 43%. Hence, our study is the first demonstrating the occurrence of family effects in ungulates neonatal predation risk.

Since in most cases the fox killed roe deer siblings after a few days' interval, we deduce that siblings are not subjected to a similar predation risk only because they share the same environmental conditions. In fact, the fox seems to adopt a win-stay strategy (Olton et al. 1981) and, after an attack to the family group, returns to the "crime scene" and, eventually, kills the surviving twins. The occurrence of family effects in predation risk is an important finding, which deserves further investigation and should be accounted for in studies regarding neonatal predation risk in ungulates.

SPATIAL DISTRIBUTION OF SMALL MAMMALS *(Manuscript IV)*

Small rodents are a keystone species in Fennoscandia. The population dynamics of several species - red fox, roe deer, hares (*Lepus timidus* and *Lepus europaeus*), black grouse (*Tetrao tetrix*), and capercaillie (*Tetrao urogallus*), are directly or indirectly affected by their abundance (Lindström et al. 1994). In particular, small rodents are the main prey for red foxes throughout their range, and the predator respond numerically to their abundance (Kjellander & Nordström 2003). We studied the distribution, abundance and species' richness of small mammals (*i.e.* voles, mice and shrews) across all available non-urban habitat types in our southern study area in order to identify areas characterised by a higher abundance of red fox main prey and, thus, by a potentially higher predation risk for roe deer fawns (*Manuscript V*).

During the course of the study, 1121 individual small mammals, belonging to 11 different species, were trapped. For the three most common species we estimated the population size in different habitat types through a capture-mark recapture analysis (Fig. 8).

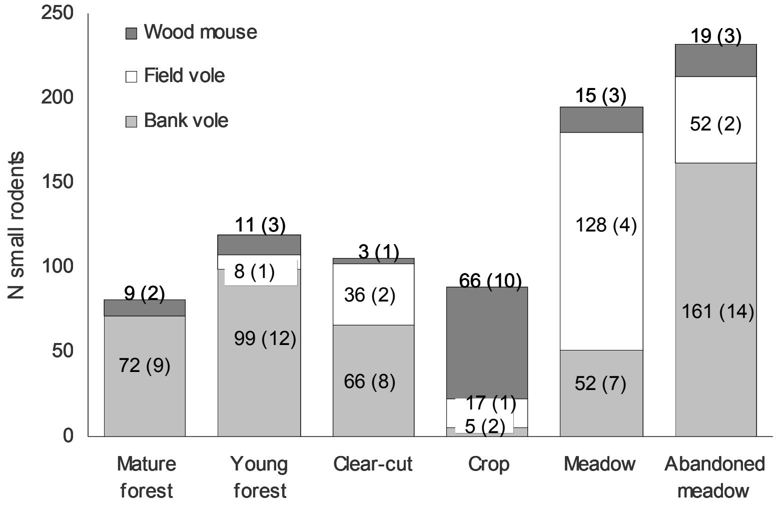

Fig. 8. Population estimates for the most frequently trapped small rodents (bank vole *Clethrionomys glareolus*, field vole *Microtus agrestis*, wood mouse *Apodemus sylvaticus*) calculated by the capture-mark-recapture analysis, in each habitat type, per area unit.

Complex and heterogeneous ecosystems support a higher diversity of ecological niches and, thus, are expected to support a higher carrying capacity for all members of small mammal communities. Nowadays pristine, continuous multi-aged boreal forests of south-eastern Norway have been converted into patchworks of agricultural areas, clear-cuts and even-aged conifer monocultures, characterised by an overall lower degree of ecological complexity. On the contrary, following the decline in livestock numbers, areas formerly used as grazing or hay meadows have been abandoned and are slowly reverting to forest, thus providing a potentially important habitat in terms of biodiversity (Staaland et al. 1998). Accordingly, agricultural areas with lowest intensity of use and highest structural heterogeneity - *i.e.* abandoned meadows - supported the highest abundance of small mammals, and may thus represent a surplus habitat (*sensu* Hansson 2002). The community was clearly dominated by *C. glareolus* in abandoned meadows and by *M. agrestis* in meadows, potentially reflecting inter-specific competition (Huitu et al. 2004) and niche separation (Hansson 1999). Mature forests and cultivated fields sustained the lowest abundance of small mammals. However, while mature forests also supported the lowest diversity, cultivated fields unexpectedly sustained the highest species diversity (Fig. 10). Only *A. sylvaticus* reached highest abundance in cultivated fields, but its marked association with edges reflected the need for landscape-scale complexity. Even though it is widely accepted that the intensification and expansion of modern agriculture is amongst the greatest current threats to biodiversity worldwide, agroecosystems in south-eastern Norway are embedded in a matrix of forested areas and agricultural lands still have the potential to attract, even though only occasionally, several generalist species. Even though clear-cuts and forests sustained an overall low abundance of small mammals, those patches of clear-cuts or forests characterised by the highest ecological complexity were able to support relatively dense populations. In fact, given the high variability within each habitat type, fine-scale vegetation parameters accounted for a higher proportion of the variance in the species' assemblage (34%, Fig. 9a) compared to coarse-scale habitat descriptors (29%; Fig. 9b). Hence, our results suggest that agro-ecosystems able to maintain a high degree of fragmentation and heterogeneity – *i.e.* meadows, shelterbelts, and riparian habitats - may provide an opportunity to conserve biodiversity in human-dominated areas. In addition we suggest that, in order to preserve abundant and diverse small mammal communities in human-dominated habitats, landscape planning, forestry and agricultural practices should actively manage for ecological complexity.

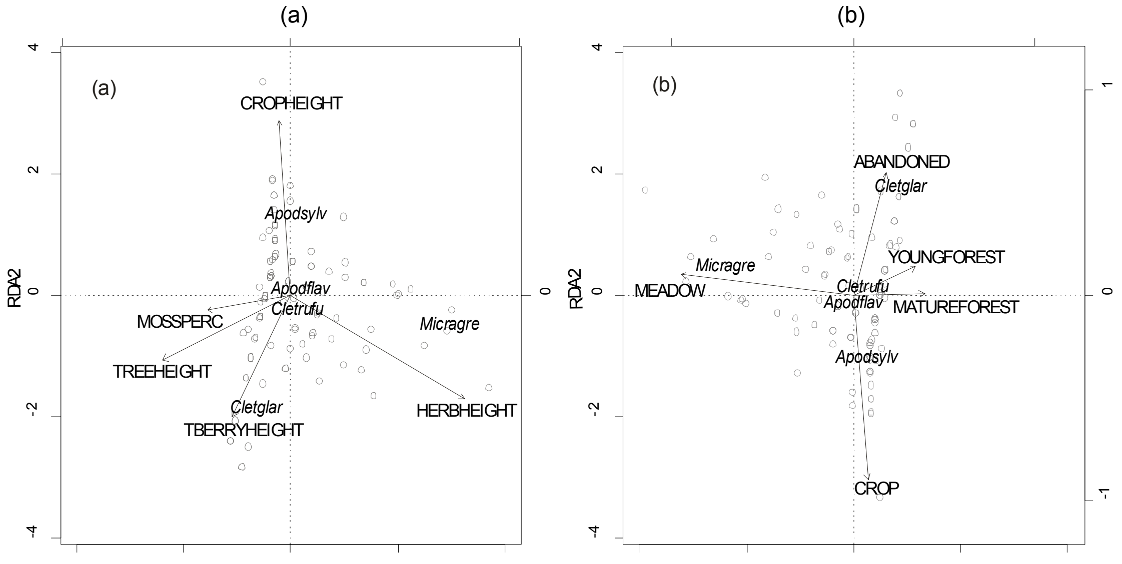

Fig. 9. Biplots of (a) stepwise redundancy analysis (RDA) illustrating the relationship between vegetation parameters (a) or habitat types (b), and the 5 most frequently trapped small rodents' species. The length and direction of each vector is proportional to the strength of the association between the environmental variables within each plot and the RDA axes. Abbreviations of the axes, in clockwise order (a): height of crop, height of herbs, height of raspberry, height of trees, percentage of moss; (b): abandoned meadows, young forest, mature forest, cultivated fields, meadows. Abbreviations of small rodent species: *Apodemus sylvaticus*, A. *flavicollis*, *Microtus agrestis*, *Clethrionomys glareolus, C. rufucanus.* For further details see *Manuscript IV*.

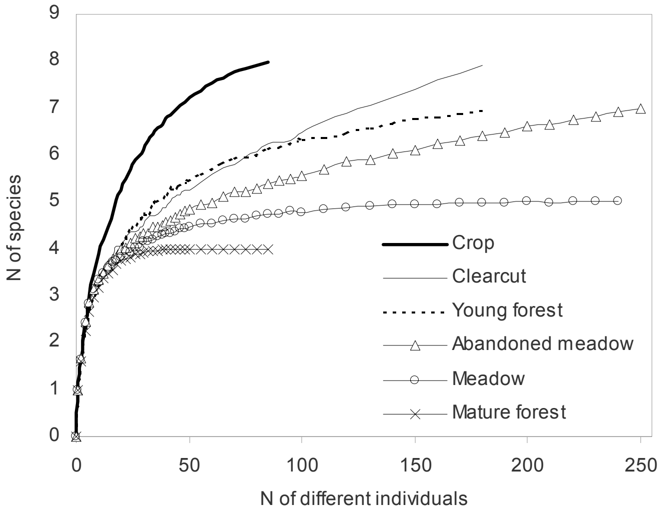

Fig. 10. Rarefaction curves illustrating how species richness increases with the number of captures within each habitat type. Each curve has been constructed by performing 1000-iteration simulation by randomly sub-sampling a growing number of individuals within each habitat type.

PREDATION RISK *vs.* DISTRIBUTION OF ALTERNATIVE PREY, FINE-SCALE HABITAT PARAMETERS AND BEHAVIOUR *(Manuscript V)*

We focused on fine spatial scales, *i.e.* within the spring-summer home range of roe deer family groups, and investigated direct and indirect mechanisms through which habitat can affect the probability of a fawn being killed by a fox. Directly, habitat characteristics may alter both prey visibility (*i.e.* detection, *sensu* Endler 1986), and the probability of a fox approaching a fawn while remaining undetected by the mother (*i.e.* approach and subjugation). Indirectly, habitat can influence prey behaviour and anti-predator behaviour, which have the potential to alter the probability of predator-prey encounter, and all the subsequent steps (*i.e.* detection, identification, approach, subjugation, *sensu* Endler 1986) leading to a successful predation event. Finally, habitat structure and composition markedly affects the distribution of the red foxes' main prey species - small rodents (*Manuscript IV*). The spatial distribution of red foxes' main prey, in turn, may affect the predators' searching behaviour, and the probability of encounters with roe deer.

Roe deer fawns adopt a hiding type of anti-predator strategy (Lent 1974), *i.e.* lie motionless, odorless, and secluded from their mothers, which keep at a certain distance in order not to attract the predators attention, and visit the offspring several times a day for care and for changing of bedding site. Hence, we expected roe deer fawns' predation risk to increase with the visibility of both mothers and fawns and with a fawn's activity index. In addition, since direct observations have shown that the defensive intervention of roe deer mothers can be important for deterring predators (Jarnemo 2004), we expected predation risk to increase with the distance between mothers and hidden fawns. Finally, we expected that roe deer fawns hiding in areas with a higher estimated abundance of the main prey of red foxes - *i.e.* small rodents -, have a higher probability of being detected by foxes and will experience a higher predation risk. A synthesis of the main predictions discussed in this paragraph is presented in Fig.1.

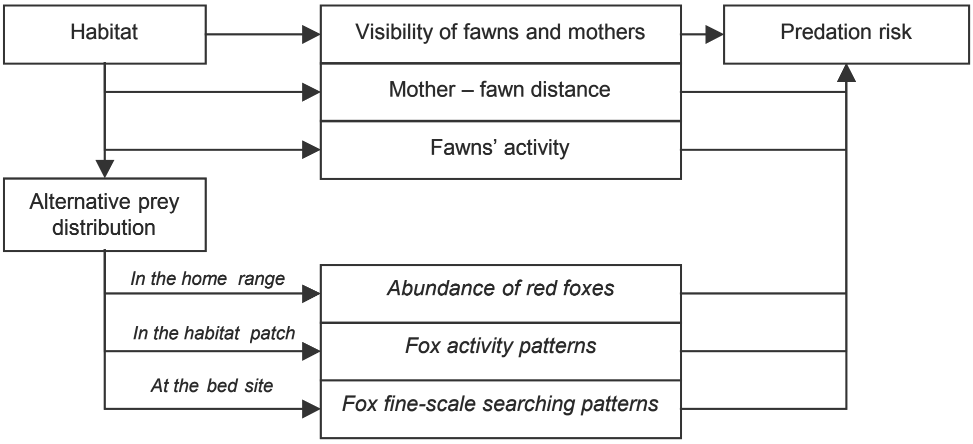

Fig. 11. Block diagram illustrating the hypotheses regarding factors affecting the probability of a roe deer fawn of being killed by a red fox. Suggested reasons underlying the hypotheses in italic.

Firstly, this study reveals the complexity of factors affecting predator-prey interactions on fine spatial scales. Predation risk was mostly affected by the visibility of the mother, which could involuntarily provide cues on the fawns' locations to sit-and-wait predators. On the contrary fawn visibility at bed sites was constantly low (on average 80 cm during the first month of life and 20 cm during the second; see also Linnell et al., 2004) and did not affect predation risk. Hence, the doe commonly succeeded in select bed sites characterized by optimal cover for their fawns but, they also have to select suitable habitat patches for the bed site simultaneously allowing them to feed, move, and rest in the surroundings of their fawns while being little visible.

During the first month of life predation risk also increased with mother-fawn distance. However, this relationship was highly context-dependent, as mother-fawn distance varied in relation to mothers' visibility, to fawns' activity, age and sex of the fawn. According to Fitzgibbon (1993), our results suggest that mothers' ability in modulating the distance to her fawn plays a fundamental role for its survival. Surprisingly, in only one case out of 421 was a fawn that would later be killed by fox found to be active when monitored during the first month of life. Activity increased from 8% to 24% of locations from the first to the second month but, considering that fawns were killed on average at age 22 days, this result does not seem to be related to the age-specific increase in activity. Activity occurred for the most part when fawns were associated with the mother and, thus, our results further support the hypothesis that roe deer doe play a determinant role in deterring the predator or defending the fawns from red fox attacks. Predation risk also increased for fawns that used bed-sites or habitat patches with a higher estimated abundance of small rodents, thus supporting the hypothesis that the distribution of main prey affects predation risk of the alternative one, but only at the age when fawns are most vulnerable.

However, among all the investigated parameters, the index of visibility of the mother was the most relevant factor explaining predation risk. This result supports previous studies indicating that the does can involuntarily provide cues on the fawns' locations to sit-and-wait predators like red foxes (Jarnemo 2004).

The type of habitat offering the lowest vegetation cover (Fig. 14) for roe deer does was crop. Accordingly, mothers used them significantly less often compared to their fawns and, when they did, the likelihood of their fawns being killed by fox increased. On the contrary, both crops and clear-cuts represented a safe place for fawns, and were used often due to the extremely low visibility index. Hence, these habitat types seemed to be used specifically by fawns in order to limit predation risk. The high selection for clear-cut, as opposed to the low selection for fields, was only due to marked differences in availability (Fig. 12). In addition, while at a higher spatial scale (above the home range, *Manuscript II*) we evidenced a strong selection for agricultural areas, at small spatial scales the selection was low due to the fact that fawns used for the most part the field edges, probably due to the high visibility of does in fields. Notice that both crops and clear-cuts are commonly very homogeneous habitat types sustaining a low abundance of small rodents and not offering any other alternative prey item for red foxes. Hence, it is not efficient to search randomly for fawns in these habitat types, and we can speculate that foxes can locate them only through cues involuntarily provided by roe deer does. Observations by Jarnemo (2004) in cultivated fields support this hypothesis.

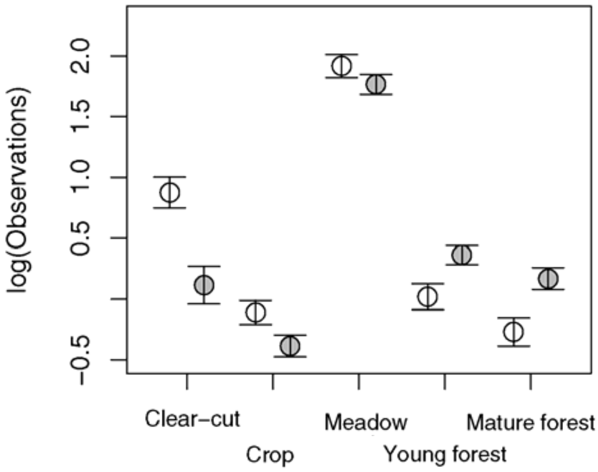

Fig. 12. Difference in roe deer habitat selection between fawns belonging to age class I (0 - 30 days, colour only) and age class II (30 - 60 days, black circle). Bars indicate standard deviation of the estimate. The estimated number of loge (observations) per habitat class refers to an average proportion of habitat availability and average sampling effort for all families.

Young forests seemed to be a rather neutral habitat type, not selected for and not particularly risky when considering the overall first month of life. However, when considering only the age when fawns were more vulnerable to fox predation, predation risk was higher in young forests. This may be related to the fact that fawns were sometimes active in young forests while the mother was not present, even though the average visibility index was rather high. The selection for young forest, as for old forest, increased from the first to the second month of life (Fig. 12) indicating that forested habitats were used at the end of the hiding phase, when fawns started following their mothers. In particular, mature forests were the optimal place where mothers and fawns could be active together, since when fawns were active their average distance was null.

Meadows were an important habitat type. Their availability in the study area was minimal (5%) but fawns' selection for them was remarkable (see also Linnell et al. 2004). However, mothers spent even more time in meadows than fawns, probably in relation to the well-known high availability and diversity of plant species, budding at different times during spring and summer (Rosef & Bele 2005). When the does were feeding in meadows, fawns were hiding close by and both their indices of visibility were on average very low. However, fawns using more meadows had a significantly higher probability of being killed by a fox both when considering the overall first month of life and, even more markedly, when considering only the most vulnerable period (Fig. 4). Why were meadows so risky? The most striking feature related with meadows was the remarkably higher abundance of small rodents preferred by fox at all spatial scales, compared to other habitat types. Hence, it is reasonable to expect a higher activity of red foxes in this habitat type.

Accordingly, fawns using more meadows, *i.e.,* those being exposed for longer time in potential "red fox hot spots", had a higher probability of being killed by a fox (Fig. 13). In particular, the use of bed sites with a higher estimated abundance of small rodents lead to a higher predation risk at the most vulnerable stage for roe deer fawns. At this stage, predation risk increased with mother-fawn distance in this habitat type. Hence, we suggest that meadows are "hot spots" for red foxes, and represent a dangerous habitat particularly if the mothers leave their fawns alone at the stage when these are most vulnerable.

When considering the family group as random effect in our analyses, none of the results discussed was significant. This further supports previous findings (*Manuscript* II) showing the existence of family effects, *i.e.* non-independence among siblings, in predation risk. Hence, our results support the suggestion that red foxes adopt a win-stay-strategy (Olton et al. 1981), and are able to track back the family group and kill the remaining fawns, irrespectively of the habitat used or the behaviour.

In conclusion, this study showed that fine-scale habitat characteristics affect predation risk mostly by determining mothers' visibility (*i.e.*, prey "detection", *sensu* Endler, 1986) and influencing predator-prey encounter probabilities, which are affected by behavioural parameters and by the distribution of red foxes' main prey. While crops and clear-cuts represented safe hiding areas for fawns, forested habitats represented areas where fawns can practise moving and interact with their mothers. Meadows were small patches rich in small rodents, which attracted red foxes and represented a risky habitat type for roe deer fawns. However, all of our results strongly support the hypothesis that the ability of roe deer does in limiting their visibility, modulating the distance to her fawn, and choosing the most appropriate habitat patches and the most safe bed sites for her fawns avoiding being predictable is crucial for their survival.

Fig. 13. Habitat used by fawns *vs*. predation risk: comparison between the habitat types recorded at the last five locations before a roe deer fawn was killed by red fox (dark bars), and the habitat type recorded at the five locations preceding the average age a fawn was killed by fox (22 ± 13 days, n = 21) - for fawns that survived (light bars). Given the non-independence among siblings in predation risk (*Manuscript II*), for each family group we only considered the first fawn that was killed by red fox.

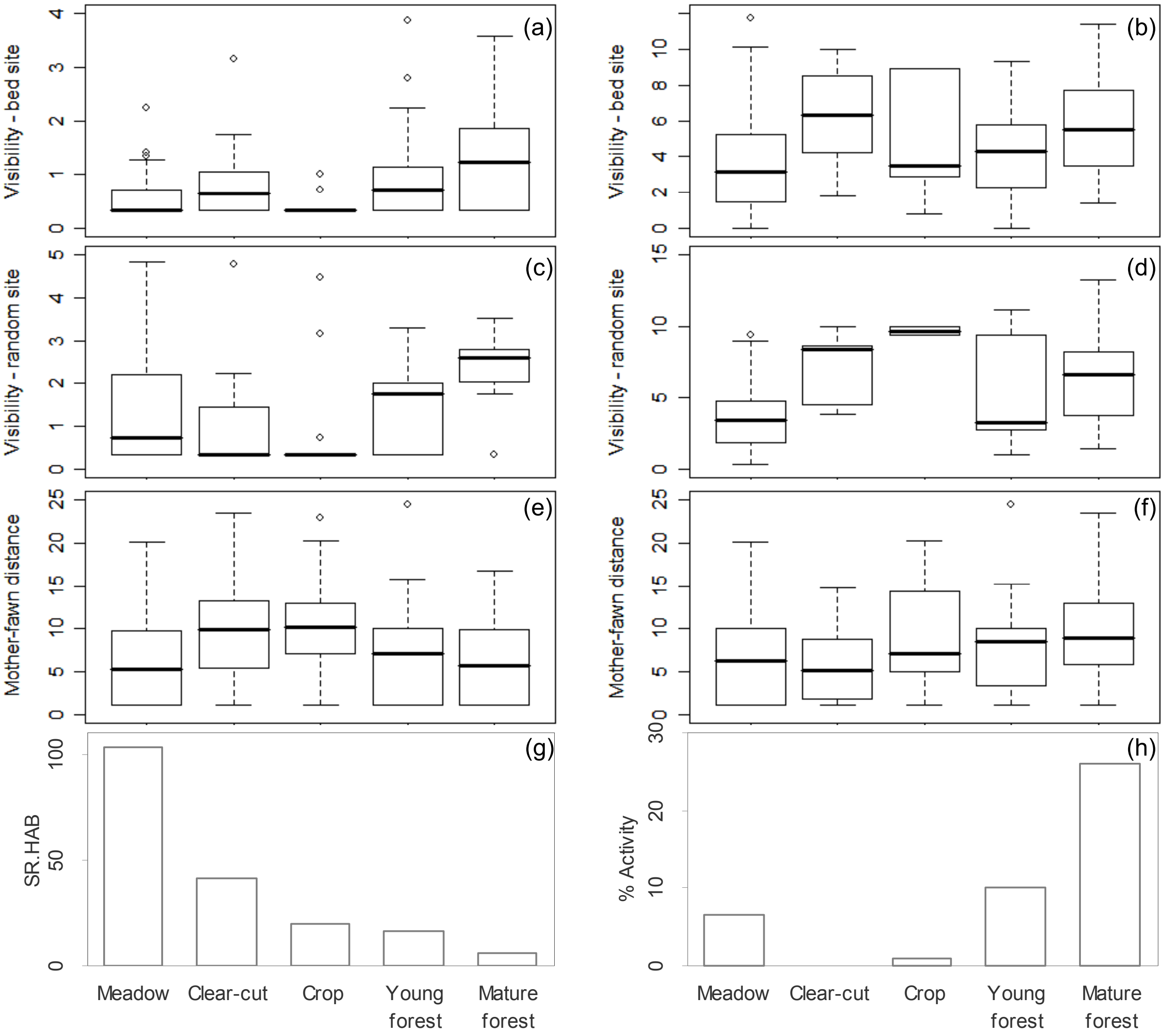

Fig. 14. Differences among habitat types in the distance between roe deer mother and their fawns (a), in the indices of visibility registered at random points (b), and at each bed site (c); figures on the right refer to the mother while those on the left refer to roe deer fawns. In addition, (d) differences among habitat types in the abundance of small rodents' species preferred by fox (SR.HAB) and (e) percentage of times a fawn was active.

CONCLUSIONS

Eight years of study on radio-monitored roe deer fawns have shown first of all that red fox predation risk is highly context dependent, and can only be investigated properly through comprehensive studies based on a multi-scale approach. Our study showed that the higher neonatal predation risk commonly observed in open habitats (Nelson & Woolf, 1987; Aanes & Andersen 1996; Jarnemo et al. 2004b) is the result of complex web of factors operating at different spatial scales (Bowyer & Kie 2006) on the populations and on the individuals.

Environmental, climatic and anthropogenic variables affect predator and prey densities and the frequency of predator-prey encounters at a regional scale, thus determining the predator functional response and the overall predation rates and patterns. Wide-scale landscape structure and composition greatly affects movement patterns, which can influence roe deer predictability and predation risk in a way determined by the ecological settings of the study area.

Within each home range, habitat structure, composition and the availability of the main prey of red foxes (*i.e.* small rodents) can affect red fox abundance and activity patterns and further influence predation risk. Finally, at a given time and place the choice of the type of habitat and of the bed site where to hide the fawn can further affect predation risk. At this fine spatial scale, the probability of a fawn being killed by red fox is affected by a complex web of interacting variables, among which visibility of roe deer does, spatial distribution of small rodents, distance between mothers and fawns, and fawns' activity.

Even though the behaviour of roe deer does is determinant for their fawns' survival, if a red fox kills one fawn, the survival probability of the remaining siblings can be compromised, regardless of the behaviour of the mother. The existence of "family effects" - *i.e.* non-independence among siblings in predation risk -, is an important finding, which deserves further investigation and should be accounted for in studies regarding neonatal predation risk in ungulates.

Considering the higher predation risk associated with agricultural areas at wide spatial scales, and with meadows, at the home-range scale, the pronounced selection agricultural areas and meadows could seem to be a non-adaptive strategy on the part of the roe deer doe. However, this habitat choice reflects the does' particularly high energetic stress due to pregnancy and lactation, as roe deer are at the end of the capital-income breeder continuum (Andersen et al. 2000). Hence, this high-risk high-gain decision is likely to have direct repercussions on the fawn's future survival probabilities. Recently several authors have demonstrated that access to high-quality resources is closely related to the body mass of fawns in winter and consequently to winter survival, age at maturity (Gaillard et al., 1993), adult body weight (Pettorelli et al., 2002, 2003) and, finally, offspring production (Nilsen et al., 2004). Hence, while fragmented agricultural areas may appear as an attractive sink (Delibes et al., 2005), they might indeed represent the key to a higher lifetime reproductive success for those fawns surviving the hiding phase.

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Tusen takk

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Manuscript I

When a generalist becomes a specialist: patterns of red fox predation on roe deer fawns under contrasting conditions

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Abstract

The red fox (*Vulpes vulpes*) functional response to roe deer (*Capreolus capreolus*) fawns was investigated in two Norwegian study areas characterised by a 26-times difference in prey densities and contrasting habitat characteristics. In the southern area, characterised by fragmented agricultural landscape and a high number of prey available per predator, the high fawns' profitability induced a red fox consumption rate closer to the specialist end in the specialist-generalist *continuum* of feeding habits. Conversely, the scarce fawns profitability in the northern forest-dominated area characterised by low prey density promoted a type-III functional response typical of archetypal generalist predators. The different functional responses produced different predation rates (25% and 13%, respectively) and patterns (highest predation risk for fawns born at the beginning or at the end of the birth season). Even though the understanding of a predator's functional response is crucial for interpreting predation rates and patterns, much remains to be understood regarding its plasticity in different ecological settings. In the fawns - fox system, this might be the key-factor for addressing unsolved questions on the adaptive value of reproductive synchrony as an anti-predator strategy. Given the flexibility of the functional response and the resulting different impact of predation with respect to birth synchrony, we suggest that reproductive synchrony evolved primarily in response to habitat seasonality, and not as anti-predator strategy.

Introduction

Even though the functional response has been theoretically recognised as a major factor determining the impact of predation on prey populations, there is still a remarkable scarcity of publications investigating factors affecting the predator consumption rates in natural ecosystems (Abrams and Ginzburg 2000; Miller *et al.* 2006). This is mostly due to the difficulties connected with the calculation of a functional response for wild species, which requires long-term studies with a good knowledge of the density of predators, of prey, and of predation rates. As a consequence of this scarcity of information, there is a risk of basing hypotheses regarding the impact of predation on prey populations on inaccurate assumptions regarding the predator functional response within the peculiar ecological settings of each study area. This might have been the case in the debate concerning the adaptive value of reproductive synchrony as an anti-predator strategy in the roe deer fawns-red fox system (Aanes and Andersen 1996; Jarnemo *et al.* 2004 a).

Widely accepted theories state that reproductive synchrony evolved in response to habitat seasonality, according to the need for setting the birth period during the time of the year which guarantees the highest survival probability for the offspring and the highest fitness for their mothers (Sadleir 1969). For some species though, offspring production can be more synchronous than expected according to seasonality alone. The most quoted hypothesis proposes that reproductive synchrony also developed as anti-predator strategy acting through group defence, predator confusion and predator satiation (Estes 1976; Frindlay and Cooke 1982; Rutberg 1987; Ims 1990 a, b; Gaillard *et al.* 1993). However, the adaptive value of reproductive synchrony as a strategy for minimising offspring predation has been theoretically shown to be dependent on the type of functional response displayed by the predator (Ims, 1990 a, b). If the prey population is exposed to a specialist predator, reproductive synchrony should favour offspring survival through predator satiation. On the contrary, a synchronised birth season would increase predation risk from a generalist predator by favouring prey switching on the part of the predator (Ims, 1990 a, b). It follows that the highest predation risk should occur at the beginning and at the end of the birth peak for situations where prey are exposed to a specialist predator, and during the birth peak when prey are exposed to a generalist predator.

These hypotheses have been partially tested by two previous studies focusing on the red fox *Vulpes vulpes* - roe deer *Capreolus capreolus* fawn system (Aanes and Andersen 1996; Jarnemo *et al.* 2004 a), but the results have not been consistent. The red fox is an archetypal generalist predator with a broad prey spectrum but with a marked preference for small rodents throughout its range (Jedrzejewski e Jedrzejewska 1992; Lindström 1994; Cavallini and Lovari 1994; O'Mahony *et al.* 1999). However, during spring the red fox becomes the undisputed major predator for roe deer fawns and accounts for up to 90% of the total neonatal mortality (Lindström *et al.* 1994; Wotschikowsky and Shwab 1994; Aanes and Andersen 1996; Carnevali, Panzacchi and Toso 1998; Kjellander and Nordström 2003; Jarnemo and Liberg, 2005). According to the theory proposed by Ims (1990 a, b), roe deer fawn vulnerability to fox predation should be highest for those individuals born during the peak in fawn availability. While the results of Aanes and Andersen (1996) supports this hypothesis, a long-term Swedish study showed that predation risk was highest for fawns born either at the very beginning or at the very end of the birth period (Jarnemo *et al.* 2004 a). Nevertheless, these contrasting conclusions do not necessarily invalidate the theories developed by Ims (1990 a, b). We hypothesise that the different predation rates and patterns observed for a given predator-prey system in different study areas are due to an adjustment of the predator functional response to the different net profitability of prey in different ecological settings.

A functional response to a given prey item depends on its net profitability (Stephens and Krebs 1986; Prugh 2005), which first of all depends on its density or, according to the recently developed ratio-dependent theories, on its relative density to predators (Akçakaya, Arditi and Ginzburg 1995; Abrams and Ginzburg 2000; Vucetich, Peterson and Schaffer 2002; Jost *et al.*, 2005). In other words, the net profitability of roe deer fawns decreases with their relative density to predators, parallel with the predator-prey encounter rate (Endler 1986). Secondly, the profitability of a prey item depends on the easiness of its detection, approach and subjugation (Endler 1986), which are affected mostly by habitat structure and behavioural parameters. For instance, the hiding strategy adopted by roe deer fawns evolved in order to limit predation risk in presence of cover (Linnell 1994; Lent 1974) and, accordingly, newborn ungulates are more vulnerable to red fox predation when selecting open, agricultural areas compared to woodlands (Aanes and Andersen 1996; Jarnemo 2004; Jarnemo *et al.* 2004 b).

According to this theoretical background, we predict that the red fox functional response is adjusted according to differences in profitability of roe deer fawns and, thus, produces different predation rates and patterns in different study areas. In order to test this hypothesis, we compare the shape of the red fox functional response and the resulting roe deer fawn predation rates and patterns in two study areas in south-eastern Norway characterised by highly different prey population densities, rather similar predator abundance, and contrasting habitat characteristics. In the southern study area, dominated by a fragmented agricultural landscape, prey density is much higher compared to the northern area where, on the contrary, roe deer density is very low and the landscape is dominated by forests. Due to the high prey profitability, we expect the red fox to start preying upon fawns early in the fawning season in the southern study area, thus severely affecting the neonatal mortality rate; here, predation risk is expected to decrease with prey availability. On the contrary, in the northern study area prey profitability is low and we expect the red fox to start preying upon roe deer fawns late in the fawning season, when prey availability becomes highest. It follows that in this study area predation risk should increase with prey availability and that, due to the limited window of opportunity during which roe deer are vulnerable to the red fox predation, the overall predation rate should be lower compared to the southern study area.

Table 1. Mortality of roe deer fawns in the northern and southern study areas during 1995-98 and 2001-4, respectively.

Study area	Mortality causes (N of fawns dead)								Mortality, % *	Fox predation rate, % †	Mortality due to fox % ‡
	Predation			Mower	Accident	Stillbirth	Disease	Not known			
	Fox	Lynx	Dog								
Southern	21	3	1	7	1	2	1	4	41.67	25.30	58.33
Northern	7	1	0	0	1	0	0	2	20.00	13.21	77.78
TOT	28	4	1	7	1	2	1	7	33.77	20.59	62.22

* Percentage of fawns that died
† Percentage of radio-marked fawns with known fate killed by fox; excluded fawns killed by mowers
‡ Percentage of known mortality causes due to fox predation

Materials and methods

Study area

The study was conducted in south-eastern Norway. Data were collected from 1995 to 1998 in Hedmark County (Åmot, Trysil, Elverum and Rendalen municipalities; an area of approximately 5000 km^2) and from 2001 to 2004 in Østfold-Akershus Counties (Ås, Aurskog-Høland, Enebakk, Høbol, Rælingen, Spydeberg, Trógstad municipalities; an area of approximately 2500 km^2). The two study areas vary in habitat structure and composition. In Hedmark, hereafter referred to as the northern study area, 88% of the landscape is covered by coniferous forests and bog, 9% by water, and only 3% by cultivated fields. The climate is continental with cold, snowy winters and warm summers. On the contrary, the southern study area is made up of a fine mosaic of agricultural areas (24%), water (11%) and forest (65%), which is both coniferous and deciduous. The climate is milder and the snow cover is less persistent compared to Hedmark County (for further information see Linnell *et al.* 1999). The differences in climatic and habitat characteristics supported a 26-times higher roe deer population density in the southern study area and a 2.8 times higher red fox abundance (Panzacchi et al., 2007). The indices of roe deer and red fox abundance were provided by the Norwegian Association of Hunters and Anglers (Hedmark, Østfold and Akershus county offices), the Office of Environmental Affairs in Hedmark county, Hedmark University College and the Norwegian Institute for Nature Research, which carried out a track count study by skiing a total of 880 km of transects in Hedmark county (Solvang, H., Strømseth, T.H., Wabakken, P., Maartmann, E., Andreassen, E., Solberg, H.O., 2004, unpublished report), and 240 km of transects in Østfold and Akershus counties (NJFF – Norges Jeger og Fiskeforbundt - Akershus and Østfold 2004, unpublished report; see Lindén *et al.* 1996) during the winters from 1995 to 2004. Eurasian lynx (*Lynx lynx*) inhabit both Hedmark and Østfold-Akershus counties and are the second most important predator for roe deer fawns. Wolves (*Canis lupus*) are also present but they never killed young roe deer; however, they have been indirectly responsible for their death by preying upon their mothers during the period of lactational dependence.

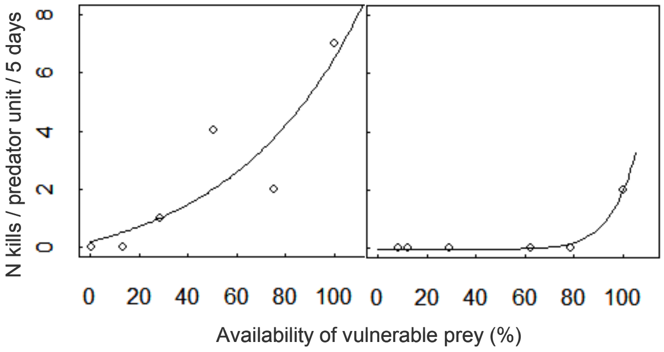

Fig. 1. Consumption rate of the red fox population in the southern (Østfold-Akershus, left) and northern (Hedmark, right) study areas during the increasing phase of the availability function of roe deer fawns in the vulnerable stage, which occurred during a 35 days period.

Captures, determination of age and of mortality causes

During the years 1995-1998 and 2001-2004 a total of 153 roe deer fawns were captured: 55 in the northern, 98 in the southern study area. Most of the fawns were captured by stalking radio-collared does, and a few were captured by chance when observing lactating mothers. All fawns were weighed at capture and 61 fawns were re-weighed an average of 6 days later in order to measure their daily growth rates. In 13 cases we were able to observe the birth date and record the weight at birth (1.427 ± 0.291 kg), which was similar to the one previously calculated in other study areas in Norway (Aanes and Andersen 1996; Andersen and Linnell 1998), Sweden (Jarnemo *et al.* 2004 a) and Italy (Pelliccioni, Scremin and Toso 2004). In the other cases, the birth dates were determined by back calculation by using the observed individual growth rates or the average observed growth rate (152 ± 0.042 g/day St. Dev., n = 60) and the average birth weight for the population. When siblings had different body masses at capture, their litter birth date was calculated by averaging their respective body masses. All fawns were equipped with an expansible radio collar. Fawns were radio-located daily during the first weeks of life in Hedmark and during the first two months in Østfold-Akershus, and thereafter they were located several times a week in order to monitor survival. Due to collar failure, we lost contact with two of the captured fawns, which were excluded from mortality analyses. Causes and patterns of mortality were studied from birth to the 25th of September, the beginning of the annual hunting season for roe deer females and fawns. The intensive monitoring plan allowed us to find the carcasses of fawns soon after death. When possible, the causes of death were determined directly in the field by inspecting the carcass (presence, size and position of bite marks) and the surrounding area (presence of tracks, scats or scent marks). When the cause of death was not obvious, the carcass was sent to the Norwegian Veterinary Institute, Oslo, for necropsy.

Table 2. Selection of the best suitable model describing the red fox functional response to roe deer fawns in the southern and northern study areas by using the Akaike Information Criterion corrected for small samples (AICc), the ΔAICc, the Akaike weights (ω) and the R^2; models with Δ < 2 are considered worthy of consideration.

Study area	Model	Formula	AICc	ΔAICc	ω	*R²*
Southern	Linear	y = a + bx	37.226	18.787	0.000	0.710
		Same, zero intercept	27.574	9.135	0.005	0.843
	Exponential	y = a (b) ^ x	18.586	0.147	0.476	*
		Same, zero intercept	**18.439**	**0.000**	**0.512**	*
	Quadratic	y = ax + bx^2	36.978	18.539	0.000	0.722
		Same, zero intercept	27.310	8.868	0.006	0.722
Northern	Quadratic	y = ax + bx^2	49.566	47.519	0.000	0.772
		Same, zero intercept	22.203	20.156	0.000	0.735
	Cubic	y = x^3	22.65	20.603	0.000	0.7143
		y = x^10 †	**2.048**	**0.000**	**1.000**	0.999

* R^2 statistic is not justified in non linear regression models. The Kolmogorov-Smirnov Goodness of fit test confirmed that the observed cumulative distribution function corresponds to the theoretical cumulative exponential distribution (z = 0.815, p = 0.519).
† Increasing the exponent of x increases the performance of the model.

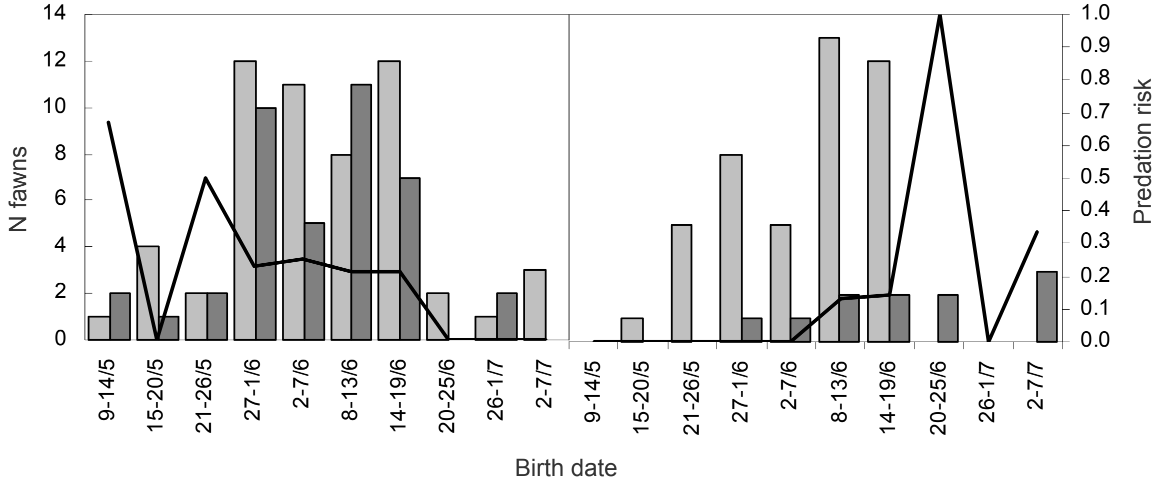

Fig. 2. Fox predation risk in relation to roe deer fawn birth date in the southern (Østfold-Akershus, left) and northern (Hedmark, right) study areas. Light and dark bars represent the number of fawns alive and dead, respectively. The lines indicate fox predation risk, calculated as the number of fawns killed by foxes in relation to the number of fawns born in each 5-days time span.

Analysis of predation risk

Age specific mortality rates were calculated using the Mayfield method (Mayfield 1961, 1975). This method is based on the consideration that individuals are not often captured on the very first day of life, and that a mortality rate calculated as the number of losses in relation to the number of captures may underestimate the actual mortality rates for the species. Hence, age specific predation rates were calculated as the number of losses in relation to fawn "exposure", which is the number of days each radio-monitored individual was actually at risk within the specified 10 days-age class (Jarnemo *et al.* 2004 a).

Considering that the probability of a fawn being preyed upon by a fox is strongly dependent on its age (Linnell, Aanes and Andersen 1995; Aanes and Andersen 1996; Jarnemo *et al.* 2004 a), and that in our study area only fawns under the age of 56 days are available as a prey for foxes, we calculated an index of prey availability during spring by using the exposure (Mayfield 1975) corrected according to the fox preference for different age classes of roe deer fawns. In order to calculate the correction factor we divided fox predation risk in each age class by the highest recorded value of predation risk. The correction factors calculated for each age class were then multiplied by the corresponding roe deer fawns' exposure in order to obtain a function representing the availability of roe deer fawns belonging to the age classes susceptible to red fox predation in the two study areas (Jarnemo *et al.* 2004 a).

Red fox functional response

The roe deer fawn - red fox system is a peculiar example of predator-prey interaction, since prey availability rapidly increases and rapidly comes to an end. We attempted to investigate the shape of the red fox functional response to the increasing availability of roe deer fawns during spring in the southern and northern study areas. The predator functional response describes how the consumption rate of individual consumers changes with respect to resource density (Solomon 1949). Since the predator *per capita* consumption rate in our study areas was unknown, we considered the total predation rate of each local red fox population, which can assumed to be stable within each study site during the short period of roe deer fawns' availability. The consumption rate was calculated as the number of fawns killed during 5-day periods by the red fox population inhabiting each study area.

The availability of prey susceptible to red fox predation changes rapidly during spring, and in order to obtain an accurate estimate of the resource density we used the previously described roe deer fawns' availability functions corrected according to the predator's preference for different age classes.

In order to select the best model fitting the observed data in each study area, we performed a series of linear and non-linear (quadratic, cubic, exponential) regression models, after having added 0.01 to all data points in order to replace the zeroes. The most parsimonious suitable model describing the functional responses was selected by comparing the Akaike Information Criterion corrected for small samples (AIC_c) and the Δ AIC_c (AIC_c for the model of interest minus the smallest AIC_c for the set of model considered) of the candidate regression models (Burnham and Anderson 2002). In addition, the Akaike weights (i.e. normalized likelihood of the models, ω_i) were calculated in order to show the relative difference in performance of each suitable model (Burnham and Anderson, 2002).

In order to assess the difference between the best models in the two study areas (in the analyses referred to as: "Area") we performed an analysis of covariance, ANCOVA, on the linearised relationship between the predator's consumption rate ("Predation") and the prey availability index ("Exposure"), and we assessed the significance of the interaction term Area*Exposure. The analyses were conducted by using the statistical software R, version 2.2.1 (R Development Core Team 2005) and SPSS statistical software for Windows, version 12.0. Parametric tests were used whenever assumptions were respected. In the results section, average values are followed by standard deviations.

Results

From birth to the 25th of September, 34 % of the 151 captured fawns died. In the southern study area mortality was more than two times higher than in the northern one (Pearson $\chi^2 = 7.339$, $df = 1$, $n = 151$, $p = 0.005$; Tab.1). Predation was the major cause of death in both areas, and the red fox's role as the predominant predator for roe deer fawns was confirmed since it was responsible for 62 % of the losses. While in the southern study area foxes killed one out of 4.0 fawns, in the northern area only one fawn out of 7.6 was preyed upon ($\chi^2 = 2.201$, $df = 1$, $p = 0.138$). Predation by lynx and dogs was of minor importance, and accounted for only 11 % of the deaths. Hay mowing-machines were the second cause of mortality (16 %); however, this additional mortality factor did not occur in the northern study area, due to the extremely low amount of fields in the widely forested-dominated landscape. The sex ratio was even at capture ($\chi^2 = 0.060$, $df = 1$, $p = 0.806$) and did not affect predation risk ($\chi^2 = 0.779$, $df = 1$, $p = 0.378$).

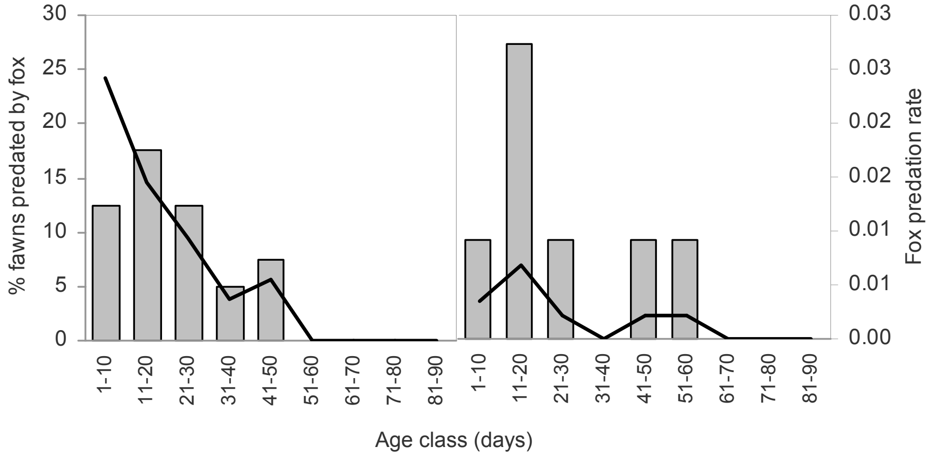

Fig. 3. Roe deer fawn predation risk with respect to age classes in the southern (Østfold-Akershus, left) and northern (Hedmark, right) study areas. Bars represent the percentage of fawns killed by red foxes at different age classes. The line shows fox predation rate calculated as the number of fawns killed in each age class in relation to the number of vulnerable radio-monitored fawns belonging to the same age class (Mayfield 1975; Jarnemo *et al.* 2004 a).

Red fox functional response

In the southern study area the predator's consumption rate (Fig. 1) was best described by an exponential curve passing through the origin (Tab 2.). On the contrary, in the northern study area the red fox did not respond to increasing prey availability until the roe deer fawn abundance index was highest. The kill rate in this study area was very low, and the functional response was best described by a function of the type: $y = x^n$ (e.g.: $y = x^{10}$, Fig. 1). The analysis of covariance showed that the functional response differed significantly between the two study areas ("Area", $F_{1/8} = 9.164$, $p = 0.016$, "Exposure", $F_{1/8} = 16.714$, $p = 0.003$, "Area*Exposure", $F_{1/8} = 6.345$, $p = 0.036$).

Factors affecting predation patterns

Birth dates

Eighty percent of the fawns were born between the 27th May to the 19th June, and the birth period (mean: 8th June; median: 9th June) was relatively constant among years (ANOVA, $F = 1.339$, $df = 7$, $p = 0.237$) and between study areas (t test, $t = -1.073$, $df = 149$, $p = 0.285$; see also Linnell and Andersen 1998). Hence, we pooled the data for further analyses. The overall fox predation risk seemed to be higher for fawns born outside the birth peak (27 May-19 June), but this trend was not significant ($\chi^2 = 0.421$, $df = 1$, $n = 151$, $p = 0.516$). When considering the two study areas separately, the trend became clearer: in the southern area fox predation risk (fawns killed by fox *vs.* survivors) tended to be higher for fawns born early in the birth season (Logistic regression, *Wald statistic* = 3.289, $df = 1$, $p = 0.070$), while in the northern area it was significantly higher for fawns born after the birth peak (*Wald statistic* = 6.477, $df = 1$, $p = 0.011$; Fig.2).

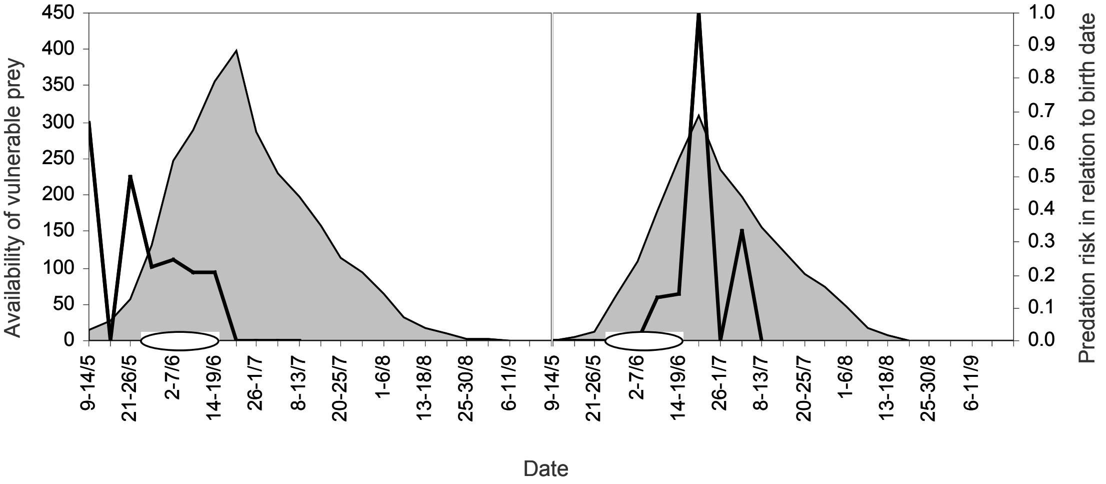

Fig. 4. Red fox predation risk (line) in relation to birth date and to the index of roe deer fawn availability in the southern (Østfold-Akershus, left) and northern (Hedmark, right) study areas. The index of availability (shaded area) was calculated as the number of fawns alive in each time interval, belonging to the age classes vulnerable to fox predation. The ellipses show the birth peak, i.e. the period during which 80% of the births occurred.

Age

On average, fawns were killed by foxes at the age of 23 ± 14 days (*n* = 28). Fawns killed by lynx lived on average 75 ± 41 days (*n* = 4), hay-mowers killed fawns at 9 ± 10 days of age (*n* = 7), and other causes of mortality (incidents, diseases, predation by dogs) occurred on average at 26 ± 22 days of age (*n* = 4; *F* = 12.742, *df* = 3, *p* = 0.000).

Fox predation rate was high during the whole first month of life and decreased only in the second month (Mann Whitney *U* = 301.000, *n* = 51, *p* = 0.011). In both study areas, the percentage of fawns killed by red foxes was highest within the age class 10 to 20 days (Fig. 3, bars). However, when fox predation rate was calculated as the number of fawns killed in each age class in relation to the number of vulnerable radio-monitored fawns belonging to the same age class (Mayfield 1975; Jarnemo *et al.* 2004), the highest predation rate occurred in the southern study area immediately after birth, while in the north it occurred between 10 and 20 days of age (Fig. 3, lines). Accordingly, while in the southern area the proportion of fawns killed by fox significantly decreased within the first 60 days of life (Fisher's exact test, *df* = 2, *p* = 0.009) in the northern study area this trend was not significant (*p* = 0.307).

Availability of vulnerable fawns

The red fox predation risk in relation to the availability of fawns belonging to the age classes preferred by fox is presented in Fig. 4. The figure shows that in the southern study area predation risk was high from the beginning of the birth season and did not significantly vary with the overall availability of fawns (*Wald statistic* = 0.602, *df* = 1, *p* = 0.438). On the contrary, in the northern study area fawns born at the beginning of the birth season, when the availability of prey in the vulnerable stage was still low, were relatively safe and predation risk increased parallel to fawn availability (*Wald statistic* = 4.984, *df* = 1, *p* = 0.026).

Discussion

This study shows that the red fox functional response to roe deer fawns can vary significantly in areas with contrasting characteristics and, consequently, can be responsible for different rates and patterns of neonatal mortality. In spite of these variations, our study corroborates the role of the red fox as the major predator of roe deer fawns in Scandinavia (Norway: Linnell *et al.* 1995; Aanes and Andersen 1996; Sweden: Lindström *et al.* 1994; Kjellander and Nordström 2003; Jarnemo *et al.* 2004 a; Jarnemo and Liberg, 2005) as is the case in central and southern Europe (Italy: Carnevali *et al.* 1998; Germany: Wotschikowsky and Shwab 1994).

In the southern, more productive study area the red fox responded to increasing roe deer fawn availability with a functional response typical of a generalist predator switching at very low prey density (Holling 1959). On the contrary, in the northern study area the red fox started preying upon the newborn ungulates only when their availability was highest, as it is expected for an opportunistic predator switching only at very high prey density (Holling 1959). Following Krivan and Eisner (2003) and Prugh (2005), we rejected a strict dichotomy between specialist and generalist predators and suggest that a single species can adjust foraging strategy in relation to prey profitability in different ecological settings. Accordingly, in our southern study area the red fox functional response to roe deer fawns was closer to the specialist end along the specialist – generalist feeders' *continuum*, while in the northern study area the red fox feeding habits perfectly matched the ones of an archetypal opportunistic generalist predator (see also O'Mahony *et al.* 1999).

We suggest that the observed difference in the shape of the red fox functional response between the two study sites was due to differences in prey profitability, which were primarily determined by roe deer abundance and by landscape characteristics (Panzacchi et al. 2007).

In the southern study area the higher abundance of fawns in each predator's home range increased the frequency of predator-prey encounters and, thus, triggered an early prey switching on the part of the red fox, and promoted a higher degree of feeding specialisation compared to the northern area. The openness of the landscape further contributed to increase prey profitability by favouring their detectability early in the season. Thus, foxes started actively hunting for the newborn ungulates from the very beginning of the birth season, and caused a higher predation risk for fawns born before or at the beginning of the birth peak. Given the limited time during which fawns are vulnerable to red fox predation, the earlier prey switch in the southern study area resulted in an overall higher impact on neonatal mortality rates.

On the contrary, in the northern study area roe deer fawns' profitability was very low due to the very low number of prey available per predator and to the widely forest-dominated landscape. Thus, in this study area an early prey switching behaviour was likely not to be cost-effective. Prey switching requires the adoption of a specific and time-consuming hunting technique, as the red fox is most successful in hunting roe deer fawns while surveying open areas, and occasional attacks carried out while conducting less prey-specific searches often fail (Jarnemo 2004). The sit-and-wait strategy however reduces the time available for capturing alternative prey items, and should therefore be adopted only when roe deer fawns represent a highly profitable item. As a consequence, in the northern study area roe deer fawns were killed for the most part when they were encountered opportunistically during the peak in prey availability and, thus, the fawns born at the beginning of the birth season were relatively safe.

We could not monitor the density of alternative prey and, thus, we cannot exclude the possibility that the lower profitability of roe deer fawns in the northern study area was due to a higher availability of alternative prey compared to the southern study area (see O'Mahony *et al.* 1999; Abrams and Ginzburg 2000; Miller *et al.* 2006). However, this hypothesis seems rather unlikely, considering the commonly higher abundance of different prey items in heterogeneous agricultural ecosystems and at lower latitudes (Andrén 1994; Kurki *et al.* 1998).

In conclusion, our study shows that a predator functional response is adjusted according to differences in profitability of prey in different ecological settings, and can thereby produce higher predation rates during or outside the peak in prey availability in different study areas. However, one issue remains unsolved. While the roe deer mean birth dates vary following a climatic gradient throughout the species' range, birth synchrony is more conservative than expected according to seasonal environmental constrains alone, with 80% of the births occurring during 24 to 30 days (Strandgaard 1972; Gaillard *et al.* 1993; Carnevali *et al.* 1998; Linnell and Andersen 1998). So, has birth synchrony an adaptive value as an anti-predator strategy? Our results suggest that the answer varies in a context-dependent way. While a higher predation rate for fawns born outside the peak should strengthen the concentration of births in areas with a high abundance (our southern study area and Jarnemo *et al.* 2004 a), a reversed situation may occur in areas with low relative prey density (our northern study area) or high relative abundance of predators (Aanes and Andersen 1996). Interestingly, in the absence of predators no effect of birth date on fawn survival was recorded (Linnell and Andersen 1998). In conclusion, we suggest that the selection pressure from red fox predation can act either toward or against a synchronous roe deer birth season in different years and/or in different areas. Hence, our results suggest that the observed disproportionately conservative reproductive synchrony recorded through out the roe deer range might have little consistent adaptive anti-predator value and might be due primarily to environmental and physiological constraints.

This interpretation supports the conclusions of an increasing number of studies (Linnell and Andersen 1998; Post *et al*., 2003; Miller *et al.* 2006), and contextualize them within the growing evidence of the flexibility of the functional response in natural ecosystems proposed by Krivan and Eisner (2003) and (Prugh 2005), and the theories regarding the predator functional response proposed by Ims (1990 a, b). On a more general perspective, our findings contribute towards filling the gap in the knowledge of factors affecting the functional response in natural ecosystems (Abrams and Ginzburg 2000), and suggest interpreting variations in predation rates and patterns in light of the plasticity of a predator's consumption rate in the particular ecological settings of each study area.

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Manuscript II

Family effects and multi-scale consequences of landscape composition on roe deer fawns’ predation risk to red foxes

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Summary

This paper aims at investigating the direct and indirect mechanisms through which forest fragmentation by agricultural land affected roe deer fawns’ predation risk to red foxes during an 8-years study of 151 radio-monitored fawns in south-eastern Norway. Given the strict association between siblings during the first months of life, we also hypothesised relatedness among siblings (i.e. family effects) in predation risk.

This is the first study demonstrating the occurrence of family effects in ungulates’ neonatal predation risk. After a fox killed one member of a family group, the probability of a sibling being killed rose from 20 % up to 43 %.

The effect of landscape structure was investigated by adopting a multi-scale approach (regions, municipalities, 5 km and 2.5 km buffers, home ranges). At most spatial scales, fragmentation by agricultural land negatively affected the distance between consecutive locations, and positively affected both roe deer and red fox indices of abundance (obtained through 1120 km transects). However, we did not detect any influence of habitat fragmentation on fawns’ growth rates. The most parsimonious model explaining predation risk, with family group as random variable, included roe deer abundance, proportion of agricultural land within 2.5 km, and fawn movements. In particular, predation risk increased with (i) forest fragmentation, which enhanced fawn detectability, (ii) roe deer abundance, due to higher prey profitability and (iii) shorter movements, which enhanced predictability.

Our study suggests that the higher neonatal predation risk observed in open habitats is an outcome of a complex interaction involving factors operating at different spatial scales. Large-scale environmental variables affect predators and prey densities and, thus, affect the predator functional response and predation rates. At a smaller spatial scales movement patterns, largely determined by environmental variables, can further affect predation risk in a way determined by the ecological settings of the study area. Finally, individual predation risk can be further affected by both local-scale habitat fragmentation and family effects. The occurrence of family effects in predation risk is an important finding, which deserves further investigation and should be accounted for in studies regarding neonatal predation risk in ungulates.

Introduction

Constant adult survival and marked variations in juvenile recruitment are characteristic features of large herbivores' population dynamics (Gaillard, Festa-Bianchet & Yoccoz 1998a). As a result, variations in population growth rates are primarily driven by changes in neonatal mortality, which is the most fluctuating and unpredictable among demographic parameters (Hewison, 1996; Gaillard *et al.*, 1998b; 2000). A great deal of the spatial variability in juvenile survival is accounted for by the mere presence or absence of predators. A literature review revealed that, in areas inhabited by predators, neonatal mortality of temperate ungulates average 50% of the production, *versus* 20 % in predator-free areas, and that predation is by far the most frequent cause of death being responsible for about 70% of the losses (Linnell, Aanes & Andersen 1995). Still, temporal and spatial variations in neonatal predation rates and patterns remain significant and, due to the limited number of long-term comparative studies on juvenile mortality, virtually unexplored. The fact that predator-prey interactions, as well as other ecological processes, are affected by factors acting at different spatial and temporal scales (Levin 1992; Bowyer & Kie 2006), further complicate their study.

Rates and patterns of predation are the outcome of the interaction between factors affecting predation risk at the community level, individual life history traits, and individual behavioural decisions. At the community scale, the basic degree of vulnerability of a given prey population is primarily determined by the composition of the predator guild (Sih Englund & Wooster 1998), the abundance of predators (Jarnemo & Liberg 2005) and prey (Ballard, 2001; Prugh 2005), the length of their sympatry (Berger, Swenson & Persson 2001), and the availability of alternative profitable prey items (Patterson *et al.*, 1998; Lingle 2000; Kjellander and Nordström 2003). In addition, temporal and spatial variations in environmental (Angelstam 1992) and climatic (Ballard, 2001) parameters alter the availability of food and cover and, thus, affect individual predation risk by promoting changes both at the community level (e.g. population density, availability of alternative prey), and in the behaviour and life-history traits of the individuals. At the individual scale in fact, neonatal vulnerability to predators can be affected by a wide range of variables such as the birth period, sex, age, weight, activity, movements and habitat use of the newborn individuals (Aanes & Andersen, 1996; Smith & Anderson 1996; Linnell & Andersen 1998; White & Berger, 2001; Jarnemo 2004; Jarnemo *et al.* 2004b; Vreeland, Diefenbach & Wallingford 2004; Panzacchi *et al.* 2007), in addition to the age, dominance rank and experience of the mothers (Byers & Byers, 1983; Fitzgibbon, 1993).

However, between the community scale and the individual scale lies an intermediate level, which may be relevant in order to understand predation processes in ungulate species and which, to our knowledge, has passed unnoticed: the family group. Most mammals produce twins or triplets which share the same genetic pool and the same ecological settings, exhibit similar movement and activity patterns, and benefit from the same maternal experience (Lent 1974; Linnell 1994; Swede, Hendrich & Wemmer 1994) for the first months of life. Indeed, an extensive study in predator-free areas demonstrated that roe deer (*Capreolus capreolus*, L. 1758) fawns belonging to the same family group have a more similar body development and, during unfavorable years, experience more similar survival rates than non-siblings (Gaillard *et al.*, 1998b). Ultimately, family effects have repercussions on the female lifetime reproductive success and on the overall roe deer population dynamic (Gaillard *et al.*, 1998b), and greatly increase the differences in reproductive success between individuals. Nevertheless, up to now the role of relatedness among individuals in predation risk has been completely overlooked. In this paper we start filling this gap by investigating the role of family effects (i.e. non-independence among siblings) on roe deer fawn's predation risk to red fox (*Vulpes vulpes*, L. 1758).

Furthermore, we focus on the multi-scale relationship between landscape structure and roe deer fawns' predation risk, both considering individuals and family groups as a unit. Lent (1974) proposed that the hiding strategy adopted by roe deer fawns evolved in order to decrease predation risk in habitats with an abundance of cover. Several studies have confirmed this hypothesis, and showed that predation risk is higher for fawns including a higher proportion of open habitat in their ranges or, within the home range, selecting bed sites in open areas (roe deer: Aanes & Andersen 1996; Jarnemo *et al.* 2004a; white tailed deer *Odocoileus virginianus*, Z. 1780: Nelson and Woolf 1987; pronghorn *Antilocapra Americana,* O. 1815: Barret 1981). The most quoted explanation for the observed patterns is a higher detectability of the fawns (Jarnemo 2004) and of their mothers, which can involuntarily give cues to a searching predator (Byers & Byers 1983; Fitzgibbon 1993). However, habitat structure and composition also affects the spatial distribution of the resources and, thus, the distribution and the abundance of predators (Kurki *et al.*, 1998) and prey (Gill *et al.* 1996), their movement patterns, and their physiological condition (Pettorelli *et al.*, 2001, 2002; Focardi *et al.*, 2001).

The aims of this paper are to investigate the direct and indirect mechanisms through which landscape characteristics at different spatial scales affect neonatal predation risk, and to determine which unit – individual fawns *vs.* family groups –should be adopted in further studies regarding predation risk in neonatal ungulates. A synthesis of the main hypotheses tested in this paper is presented in Fig. 1.

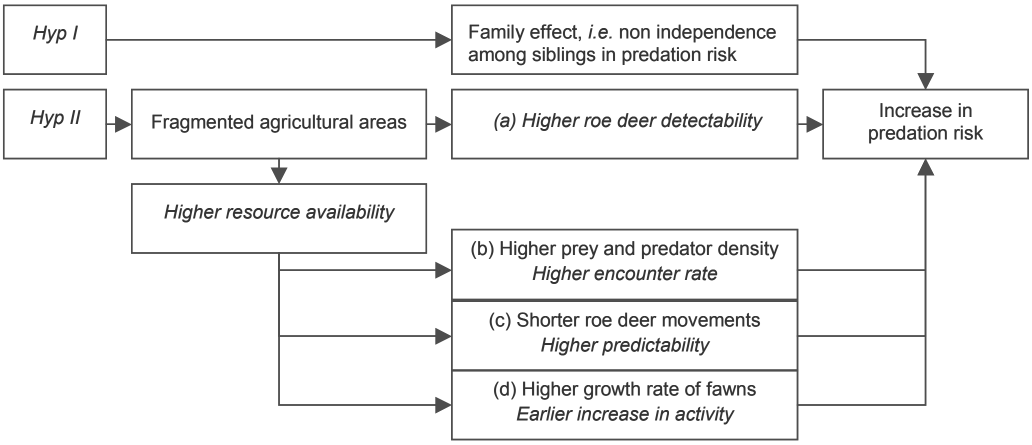

Fig. 1. Block diagram illustrating the hypotheses tested in this paper regarding factors affecting the probability of a roe deer fawn of being killed by a red fox. The suggested reasons underlying the hypotheses are in italic.

Study area

The study was conducted in south-eastern Norway. Roe deer fawns were studied from 1995 to 1998 in Hedmark county, hereafter referred to as the northern part of the study area (Linnell *et al.*, 1999) and from 2001 to 2004 in the neighbouring counties of Østfold and Akershus, referred to as the southern part of the study area (Fig. 2). The study area encompasses a gradient in latitude, climatic conditions and habitat structure. In the northern part of the study area 88% of the landscape is covered by coniferous forests, 9% by water, and only 3% by cultivated fields; the climate is continental with cold, snowy winters and warm summers. On the contrary, the southern part of the study area is made up of a fine mosaic of agricultural areas (24%), water (11%) and forests (65%); the climate is milder and the snow cover is less persistent compared to the northern area. Red foxes were the main predator for roe deer fawns followed by Eurasian lynx (*Lynx lynx*); wolves (*Canis lupus*) are also present in the study area.

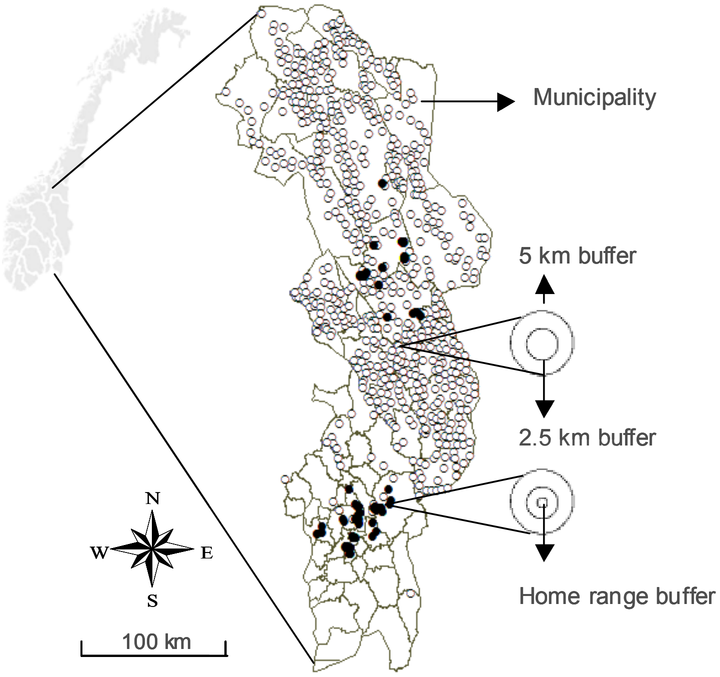

Fig. 2. Location of the study area in south-eastern Norway (left), encompassing Hedmark, Østfold and Akershus counties (respectively, from north to south), and study design (right). Each dark dot represents the centre of activity of one radio-monitored roe deer family group; circles indicate the location of transects used for estimating the indices of abundance of red fox and roe deer. The study was carried out by adopting a multi-scale approach, and landscape characteristics were investigated in the area surrounding each roe deer family group and each transect at the Municipality scale, and within buffers with a radius equal to 5 km, 2.5 km, and within a home-range buffer.

Methods

Capture and radio-monitoring of roe deer fawns

A total of 151 roe deer fawns (55 in the northern, 98 in the southern study area) belonging to 83 different family groups were captured after birth and provided with expansible radio-collars. In order to maximise the chance to detect and capture all siblings composing a family group, fawns were captured by stalking radio-collared does or lactating mothers. When only one fawn was captured, the surrounding area was searched in order to find a sibling. Nevertheless, some mortality might have occurred before the capture took place; thus, the overall mortality is likely to be underestimated. All fawns were weighted at capture and in 61 cases they were re-weighed on average after 6 days in order to measure their daily growth rate. Every fawn was radio-monitored approximately every day for the first two months of life in order to record daily movements and mortality causes. Causes of death were assessed directly in the field or at the Norwegian Veterinary Institute, Oslo. From birth to the 25th of September, 34% of the radio-monitored fawns died, and predation by red fox was the major cause of death accounting for 55% of the losses.

Family effects

We tested for family effects on individual risk of predation by adapting a method originally developed by Gaillard *et al.* (1998b) in order to test for family effects on growth rate and survival. At first, we calculated roe deer fawn survival probabilities in the two study areas as the proportion of individuals that survived for twins (S_w) and for triplets (S_t). Given the null hypothesis that there are no family effects, the probability of a fawn surviving (P_a) or dying (P_d) in a family composed by twins and by triplets is given by:

For twins:
$P_{aa} = S_w^2$
$P_{dd} = (1 - S_w)^2$
$P_{a,d} = 2S_w (1 - S_w)$

For triplets:
$P_{aaa} = S_t^3$
$P_{ddd} = (1 – S_t)^3$
$P_{aa,d} = 3S_t (1 – S_t)^2$
$P_{a,dd} = 3 S_t^2 (1 – S_t)$

In order to calculate the number of families expected to belong to each of the above-mentioned categories, we multiplied each probability for the total number of families sampled in each subset. Then, we tested for the hypothesis that the probability of observing a family in which either all fawns or two out of three fawns are killed by fox is higher than the probability of obtaining a family in which one fawn out of two, or two fawns out of three survived ($P_{dd} + P_{ddd} + P_{dda} > P_{ad}\ P_{aad}$). Expected and observed values were compared using a chi-square statistic.

Roe deer and red fox abundance

Wildlife censuses, predominantly aimed at large carnivores, were carried out in south-eastern Norway (Fig. 2) by the Norwegian Association of Hunters and Anglers (Hedmark, Østfold and Akershus county offices), the Office of Environmental Affairs in Hedmark county, Hedmark University College and the Norwegian Institute for Nature Research, starting from 1995. Indices of red fox and roe deer density were available as a by-product of these monitoring activities. The number of tracks crossings the transects were recorded while skiing along 3 km linear transects for a total of 880 km in Hedmark (Solvang *et al.* 2004, unpublished report; Linnell *et al.*, in press), and 12 km triangular transects for a total of 240 km in Østfold and Akershus (see Lindén *et al.* 1996). Following Kurki *et al.* (1998) we considered the number of tracks /km/24 hrs, corrected for the number of days after the last snowfall, as an index of abundance. In Finland the track index calculated by using wildlife triangles reflected the fox density estimates calculated from hunting data (Kurki *et al.* 1998) and, in our study area, the number of roe deer shot in each municipality closely reflected the number of tracks observed. Since in Hedmark the track count study started in 2003, when the local red fox population was recovering from a sarcoptic mange epidemic, the index of red fox abundance was corrected by following the Official Hunting Statistic of Norway (2004), which documented a 17% increase in the number of red fox shot in 1995-1998, compared to 2003-2004. The indices of red fox and roe deer abundance were, respectively, 2.8 times and 26 times higher in the southern part of the study area compared to the northern one.

Landscape effect on roe deer and red fox abundance

By using a digitised map we focused on two landscape descriptors that we hypothesised would be relevant for the ecology of roe deer and red fox: the proportion of fields with respect to forest (field area / [forest + field] areas) and an index of habitat fragmentation ([field + forest edges]/area unit). Given that a key-problem in habitat studies is the definition of the relevant spatial scale explaining the ecological process of interest (Levin 1992), we followed Kurki *et al.* (1998) and adopted a multi-scale approach. The relationship between landscape composition and the abundance of roe deer and red fox tracks was investigated at a wide spatial scale (municipality) and within two smaller buffers of different radii (5 km and 2.5 km) centred in the middle of each transect (Fig. 2). We chose the size of the radius by following Kurki *et al.* (1998), who found a significant relationship between habitat composition and red fox abundance at several spatial scales, with the strongest relationship occurring within a 5 km - radius. Since in our study area an average red fox home range extends over about 5 km^2 (Panzacchi *et al*., 2007), as the size of the buffer centred on the transects decreases, we assume that the track index becomes more representative of individual red fox activity, rather than population abundance.

Landscape effect on movements, growth rate and predation risk

For these analyses we applied the same principles discussed in the previous session, with the 5 km and the 2.5 km buffers centred in the geometric centre of activity of each family group. The geometric centre of activity was calculated by considering only radiolocations collected during the period when fawns are susceptible to fox predation, which, in our study area, occurred up to 56 days of life. In order to better investigate the landscape actually available for each family group, we created a third buffer whose radius was equal to the radius of the average first-56-days home range calculated for each family group. Since home ranges in the southern study area ($\overline{x}$ = 0.362, 95 km^2, 95% CI, lower bound: 0.292, upper bound: 0.493, n = 36) were much smaller than the ones in the northern area ($\overline{x}$ = 1.468 km^2, lower bound: 0.906, upper bound: 2.030, n = 22; Mann Whitney, U = 125, $p < 0.001$), we built buffers with different radii in the two study areas: 396 m in the southern part of the study area, and 804 m in the northern part. A major problem when investigating the effect of habitat on predation risk of juveniles is that these are often killed soon after birth, before enough locations are available in order to calculate a home range and the habitat used within. The use of home range buffers allowed us to overcome the problem by associating the predation event to the habitat characteristics within the area surrounding the birthplace.

Statistical analyses

Logistic regression models were used in order to investigate the effect of different explanatory variables on the fawns' predation risk (killed *vs.* not killed), while the relationship between landscape characteristics and roe deer fawns' growth rates, movements, or the indices of abundance of roe deer and red fox was investigated by using generalised linear models. In order to obtain normality, the distances between consecutive locations were square root transformed, and the average distance moved per individual was log-transformed. In order to rank the relative importance of each explanatory variable, we performed models including all the candidate parameters, and we assessed the relative performance of each suitable model containing only one single variable by comparing their Akaike Information Criterion corrected for small samples (AICc). Models with Δ AICc < 2 were considered worthy of consideration, and their relative difference in performance was given by the normalized likelihood of the models (Akaike weights, ωi; Burnham and Anderson, 2002).

We tested for a possible influence of sex on the probability of a sibling being killed by red fox by performing a mixed effect model with family group as a random factor. We also tested for a possible indirect effect of sex on individual predation risk operating through different activity patterns. Given the presence of pseudo-replication, we performed a linear mixed-effects model by considering the distance moved between consecutive locations as a response variable, “Sex” and “Age” as fixed factors, and the individual id-number as random factor, with data grouped by study area. Given the relevant influence of family effects and the differences detected between the northern and southern part of the study area (see results), in order to find the best model describing predation risk we performed a generalised linear mixed effect model with “Family” as a random factor nested in “Area”. Only variables whose coefficient of determination was < 0.3 were used in the models. Model selection was based on AIC_c, and the performance of the most parsimonious models was compared to the one of the null model (i.e. containing only the intercept).

Unless otherwise stated, average values are followed by standard deviation. All analyses were conducted using R 2.2 Software (R Development Core Team, 2004).

Results

Family effects

In order to test for family effects on predation risk we considered only data from families (n = 43) composed by twins or triplets for which the fate of each fawn was either “alive” or “killed by red fox”; thus, we excluded families including fawns that died for causes other than fox predation, or whose fate was unknown. The probability of observing families where either two out of three fawns or all siblings were killed by fox was higher than expected under the null hypothesis of no family effect ($\chi^2 = 4.578$, df = 1, p = 0.032). Considering all fawns with known fate and known causes of death (n = 143), red foxes killed 1 fawn out of 5.1. However, considering only those fawns (n = 25) belonging to families experiencing predation events, and in which the fate of all siblings was known, the situation changed: after one sibling was killed by fox, one out of 2.3 of the remaining siblings were killed too. Except for one case - when 35 days elapsed between the predation of two siblings - predation events within the same family group occurred on average within 4.6 days.

Landscape characteristics vs. predation risk

In table 1 we present the relationship between roe deer fawns’ predation risk and two indices of forest fragmentation by agricultural land at different spatial scales. The probability of each individual fawn being predated by a fox increased with habitat fragmentation within the home range and with both the abundance of agricultural land and of field-forest edges within the municipality. None of the candidate explanatory variables explained predation risk when considering the family group as a unit. However, the probability of detecting statistically significant patterns is remarkably reduced when considering the family as a unit, because the sample size is more than halved.

Table 1. Effect of landscape characteristics on the risk of a roe deer fawn (a) or of at least one member of a family group (b) of being killed by a red fox in south-eastern Norway. The relationship between predation risk and landscape fragmentation by agricultural areas was investigated within each Municipality, within buffers with 5 km and 2.5 km radius, and within each roe deer fawn's home range. Best performing logistic regression models ($\Delta AIC_c < 2$) with significant p-values in bold characters. Number of parameters, $k = 2$.

Landscape characteristics	Scale	(a) Individual predation risk (df = 127)					(b) Predation risk in families (df = 60)				
		AIC$_c$	ΔAIC$_c$	ω_i	z	p	AIC$_c$	ΔAIC$_c$	ω_i	z	p
Proportion of fields	Munic.	132.313	**0.053**	**0.338**	**2.489**	**0.013**	70.755	0.766	0.199	1.224	0.220
	5 km	137.069	4.809	0.031	1.231	0.218	71.920	1.931	0.111	0.582	0.561
	2.5 km	138.222	5.962	0.018	0.598	0.550	72.172	2.183	0.098	0.290	0.772
	HR	138.386	6.126	0.016	0.439	0.661	72.256	2.267	0.094	0.037	0.970
Fragmentation	Munic.	133.371	**1.111**	**0.199**	**2.200**	**0.028**	70.876	0.887	0.187	1.152	0.249
	5 km	136.764	4.504	0.036	1.332	0.183	71.941	1.952	0.110	0.559	0.576
	2.5 km	138.568	6.308	0.015	-0.251	0.802	72.119	2.130	0.101	-0.369	0.712
	HR	132.260	**0.000**	**0.347**	**2.445**	**0.015**	69.989	0.000	0.292	1.479	0.139

Table 2. Results of generalised linear models explaining the indices of abundance of roe deer and red fox with landscape characteristics at different spatial scales in south-eastern Norway ($k = 2$). Best performing models and significant p-values in bold characters.

Landscape characteristics	Scale	(a) Fox (df = 441)						(b) Roe deer (df = 156)					
		AIC$_c$	ΔAIC$_c$	ω_i	t	R^2	p	AIC$_c$	ΔAIC$_c$	ω_i	t	R^2	p
Proportion of fields	Munic.	339.271	17.693	0.000	1.881	0.005	**0.060**	206.457	15.003	0.000	1.939	0.024	**0.054**
	5 km	321.578	**0.000**	**0.700**	**4.653**	**0.047**	**< 0.001**	191.454	**0.000**	**0.533**	**4.436**	**0.113**	**< 0.001**
	2.5 km	324.379	2.801	0.172	4.329	0.041	**< 0.001**	191.756	**0.302**	**0.458**	**4.398**	**0.111**	**< 0.001**
Fragmentation	Munic.	340.522	18.944	0.000	-1.512	0.005	0.131	209.686	18.232	0.000	-0.726	0.003	0.469
	5 km	325.096	3.518	0.120	4.242	0.039	**< 0.001**	201.601	10.147	0.003	2.957	0.053	**0.050**
	2.5 km	330.672	9.094	0.007	3.500	0.027	**< 0.001**	200.847	9.393	0.005	3.088	0.060	**0.050**

Table 3. Relative effect of the average index of roe deer and red fox abundance within each Municipality on roe deer fawn's predation risk considering both the individuals (a) and the family group (b) as a unit. Selection of the best logistic regression model containing only one explanatory variable (*k* = 2). Best performing models and significant p-values in bold characters.

Response variable	Explanatory variables	AIC_c	ΔAIC_c	ω_i	z	p
(a) Individual predation risk	Roe deer abundance	**130.633**	**0.000**	**0.973**	**2.859**	**0.005**
(df = 144)	Red fox abundance	137.808	7.175	0.027	0.880	0.379
(b) Family predation risk	Roe deer abundance	**70.331**	**0.000**	**0.715**	1.382	0.167
(df = 60)	Red fox abundance	**72.172**	**1.841**	**0.285**	0.292	0.771

Roe deer and red fox abundance vs. landscape and predation risk

The index of abundance of red fox was positively correlated with both the availability of agricultural land and with habitat fragmentation at most spatial scales (Table 2a), but the parameter which best explained predator abundance was the proportion of fields within the 5 km buffer. The index of abundance of roe deer (Table 2b) followed a similar pattern and was best explained by the proportion of fields within the 5 and 2.5 km buffers. Since the transects used for the track count study were not necessarily placed within roe deer fawns' home ranges, we could only test for direct effects of predator and prey abundance on predation risk at the municipality scale. Individual predation risk was positively affected by the average abundance of roe deer within each municipality, but not by the red fox abundance (Table 3a). When considering the family group as a unit, the parameter that better explained predation risk was the roe deer abundance, even though the relationship was not statistically significant (Table 3b).

Growth rate vs. predation risk

The average observed growth rate (152 ± 0.042 g/day, n = 60) did not differ between the two sexes (t test, t = -0.947, df = 57.583, p = 0.348) nor between the southern and the northern part of the study area (t = 0.306, df = 58.961, p = 0.760), and was not explained by any of the investigated landscape characteristics (Table 4a), nor with the indices of abundance of roe deer ($R^2 = 0.200$, p = 0.374, n = 5) or red fox ($R^2 = 0.300$, p = 0.312) within the municipalities. Contrary to our expectations, predation risk was not affected by individual growth rates (t = 1.517, df = 29.84, p = 0.140). We also tested for differences in predation risk between 16 siblings with different weights at capture, and we concluded that within each family group (n = 7) the relative weight at capture did not affect the probability of a fawn being predated by fox (Wilcoxon signed ranks test, Z = -0.119, p = 0.906).

Movements vs. predation risk

We previously demonstrated that sex ratio was even at capture and that there was no significant sex - bias in predation risk (Panzacchi *et al.*, 2007). Here we tested for a possible indirect effect of sex on individual predation risk through altered movement patterns. In the first 56 days of life individual movements differed greatly between the southern ($\bar{x}$ = 265 ± 224 m, n = 1171) and the northern part of the study area ($\bar{x}$ = 530 ± 450 m, n = 568; t = 19.267, df = 1417, p < 0.001), but did not increase significantly with age (t = 0.950, p = 0.342), nor were affected by sex (t = 0.008, p = 0.938). The index of mobility of each individual fawn and of each family group was negatively affected by forest fragmentation by agricultural areas at most spatial scales (Table 4b, c). Logistic regression analyses showed that predation risk was negatively affected by the index of mobility both considering the individuals (z = -2.389, df = 119, p = 0.017) and the family group (z = -2.192, df = 60, p = 0.028) as a unit. However, the relationship between individual movements and predation risk was not significant in the southern part of the study area (northern area, z = -2.110, df = 48, p = 0.035; southern area, z = -0.700, df = 70, p = 0.484).

The most parsimonious mixed effect model explaining individual roe deer fawn's predation risk, with "Family" as a random factor nested in "Area", included proportion of fields the 2.5 km scale, roe deer density index and movements (Table 5).

Discussion

This is the first study documenting the occurrence of family effects in ungulates' neonatal predation risk (hypothesis I). After a fox killed one member of a family group, the probability of a sibling being killed rose from 20 % up to 43 %. The multiplicative effect due to the non-independence between siblings in predation risk may contribute to explaining the marked difference in neonatal mortality rates commonly observed between areas with and without predators (Linnell *et al.* 1995). However, the existence of family effects in predation risk is an important finding which deserves further investigation and should be accounted for during future studies of neonatal mortality in ungulates.

Our data can provide only a few cues for the understanding on the reasons underlying the occurrence of family effects in neonatal predation risk. Although the red fox is well known for its capability of surplus killings (Kruuk 1972), e.g. when attacking broods of ground-nesting birds (Sonerud 1985), in only two cases were roe deer siblings killed or injured during the same day and, most commonly, a few days elapsed between predation events. First of all, this supports the observations of Jarnemo (2004), and suggests that roe deer mothers play an important role in deterring the predator, at least from consecutive attacks. Secondly, this suggests that siblings are not subjected to a similar predation risk only because they share the same environmental conditions (Gaillard *et al.* 2003), are raised by the same mother (Jarnemo 2004), and adopt similar movement and activity patterns (Linnell 1994; Swede *et al.* 1994). The short time between consecutive predation events indicates that, after an attack to the family group, the red fox returns to the "crime scene" and, eventually, kills the surviving twins. Hence, both deterministic factors related to the ecological settings and behavioural parameters on the part of both prey and predators might contribute producing the observed pattern of non-independence between siblings in predation risk. The win-stay strategy (Olton, Handelmann & Walker 1981) has been documented also for several birds of prey and carnivorous mammals such as the mink (*Mustela vison*; see Sonerud 1985 and references therein), and it is an efficient hunting tactic for exploiting clumped prey moving little distances (Mitchell and Lima 2002). Roe deer twins and triplets are, indeed, clumped prey moving little distances. And movements are, actually, one of the most important parameters explaining predation risk in this study.

Geist (1982) suggested that ranging movements in ungulates decrease as resource availability increases. This should be particularly evident in the case of roe deer fawns, whose movement patterns are driven by the high energetic requirements of their income-breeders lactating mothers (Clutton-Brock, Albon & Guinness 1989; Andersen *et al.* 2000). Indeed, our results show that the inter-fix distances were strongly negatively affected by the proportion of fragmented agricultural land at all spatial scales, and in the southern, more productive part of the study area the home ranges were half the size of the ones in the northern area. In addition, previous investigations showed that in our study area roe deer activity was concentrated in proximity of cultivated fields, and was markedly higher within 250 m from the edges compared to the inner part of the forest (Bunnefeld *et al.*, 2006; see also Tufto, Andersen & Linnell 1996). As expected, restricted movements in proximity of spatially clumped resources resulted in an increased roe deer fawns' predictability and, thus, in a higher predation risk (hypothesis II. c). However, this pattern was significant only in the northern part of the study area, where the very few, small cultivated fields, scattered within a widely homogeneous, forest-dominated landscape, remarkably enhanced roe deer fawns spatial predictability. In the southern part of the study area, characterised by a highly fragmented landscape and by a much higher prey density, the beneficial effect of movements for reducing the risk of predation was lowered. We suggest that, depending on the landscape structure and composition, on predators and prey density, on their patterns of resource utilisation, and on the predator's functional response, movements may either enhance predation risk by increasing the probability of predator-prey encounters (Ozoga and Verme 1986) or, on the contrary, decrease it by reducing prey predictability (this study; Byers, 1997; Mitchell & Lima 2002; Raganella Pelliccioni, Amadesi & Toso 2003; Lima and Dill, 1990).

Not only the activity of prey was higher in the ecotone belts, but also the abundance of red fox tracks increased with habitat fragmentation and, consequently, roe deer fawns' predation risk followed a similar pattern (hypothesis II.a). Edges may increase the vulnerability of typical ecotone-species such as the roe deer by simply representing physical barriers forcing the predators to move along them. In addition, Jarnemo (2004) showed that the hunting technique leading to the highest number of successful predation events on roe deer fawns was the sit-and-wait strategy, with the red fox surveying open areas from the forest edges. From this position, the predator could spy the interactions between roe deer does and their fawns, and plan the most appropriate strategy for approaching and launching a successful attack without being deterred by the mother (Jarnemo, 2004). On a more general perspective, the widespread increase in predation risk by generalist predators with habitat fragmentation has been attributed by several authors to a numerical response of the predator to the great abundance and diversity of prey associated with ecotones (Oehler and Litvaitis 1996; Andrén 1994, 1995; Andrén and Agelstam 1988; Angelstam 1986). In view of our results an of the above-mentioned evidences of an edge-effect on predation risk, we suggests that in areas inhabited by predators, fragmented agricultural land constitute an attractive sink (Delibes, Gaona & Ferreras 2005) for roe deer.

Even though at a wide scale (i.e. municipality) both red fox and roe deer were more abundant in fragmented agricultural areas (see also Kurki *et al.*, 1998; Wahlström and Kjellander 1995, Andersen and Linnell 2000), this pattern was far more marked in the latter species than in the former one. Hence, in our study area predation risk seemed to be only marginally associated with an increase in red fox abundance, and was mostly accounted for by changes in roe deer density (hypothesis II.b). A higher prey abundance enhances roe deer fawns' profitability due to both an increased frequency of encounters between red fox and the newborn prey, and to a higher probability of observing adult roe deer, which may unconsciously reveal the offspring location (Byers and Byers, 1983) and favour an early prey switching behaviour (Panzacchi *et al.*, 2007). Indeed, we have previously demonstrated that the red fox's functional response was adjusted according to roe fawns' profitability and, thus, produced different predation rates and patterns in the northern compared to the southern part of the study area (Panzacchi *et al.*, 2007).

Contrary to our expectations, we found no relationship between landscape characteristics, roe deer fawn growth rate, and predation risk (hypothesis II.d). This result is not consistent with previous studies, which documented spatial variations in life-history parameters induced by environmental heterogeneity (Pettorelli *et al.*, 2001), and may be due to a relatively limited sample size. However, the fact that fox-killed fawns had the same body mass as surviving individuals has been also documented by Aanes and Andersen (1996), and supports the hypothesis that red fox predation on roe deer fawns is additive (Lindström *et al.*, 1994; Jarnemo *et al.*, 2004b).

In conclusion, our study suggests that the higher neonatal predation risk commonly observed in open habitats (Nelson and Woolf, 1987; Aanes and Andersen 1996; Jarnemo *et al.* 2004 a) is the result of a complex interaction involving factors operating directly and indirectly at different spatial scales (Bowyer and Kie 2006). Environmental, climatic and anthropogenic variables affect predators and prey densities at a regional scale and, thus, determine to a great extent the predator functional response and the overall predation rates and patterns (Panzacchi *et al,* 2007). At smaller spatial scales individual movements, which are primarily driven by landscape structure and by the energetic constraints of the does, can further affect predation risk in a way determined by the ecological settings of the study area. Finally, at a given time and place, the probability of a fawn being killed by a red fox can be further affected by local-scale (i.e. home range) habitat fragmentation, and by the fact that a sibling has been previously killed by a red fox.

Gaillard et al (1998b) previously documented the occurrence of family effects on the early body development and survival of juvenile roe deer in two areas without predators. These effects led to an increased variance in recruitment among females and, given the high site fidelity and the consequently high constancy in the quality of the home range and in the phenotypic qualities of the mothers inhabiting it, the authors suggested that most individuals in a stable population are descendants from only a few successful families – i.e. the ones inhabiting the best quality ranges (Gaillard *et al.*, 1998b; Nilsen *et al.* 2004). However, most roe deer populations throughout the range coexist with red fox, and Jarnemo *et al.* (2004a) showed that the reproductive success of females inhabiting home ranges with high-quality forage was highest only in years with low red fox density, while the situation was reversed when high predation rates occurred. Hence, in the presence of predators the trade-off between high-quality forage and predation risk complicates the scenario outlined by Gaillard et al (1998b) and, eventually, it may lead to roe deer populations characterised by a higher genetic variability compared to the one recorded in predator-free areas. The occurrence of family effects in predation risk may strengthen this process and further enhance the genetic variability within the population.

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Table 4. Effect of landscape characteristics at different spatial scales on roe deer fawns' growth rate (a), on the index of individual movements (b), and on the index of family movements (c); *k* = 2. Best performing linear models and significant p-values in bold characters.

Landscape characteristics	Scale	(a) Growth rate (df = 59)						(b) Individual movements (df = 128)						(c) Family movements (df = 67)					
		AIC$_c$	ΔAIC$_c$	ω_i	t	R^2	p	AIC$_c$	ΔAIC$_c$	ω_i	t	R^2	p	AIC$_c$	ΔAIC$_c$	ω_i	t	R^2	p
Proportion of fields	Munic.	-226.269	**0.360**	**0.122**	-0.229	0.000	0.820	199.950	22.094	0.000	-5.708	0.203	< **0.001**	404.886	74.997	0.000	-4.397	0.224	< **0.001**
	5 km	-226.254	**0.375**	**0.122**	0.194	0.000	0.847	192.751	14.895	0.001	-6.460	0.246	< **0.001**	402.074	72.185	0.000	-4.788	0.255	< **0.001**
	2.5 km	-226.297	**0.333**	**0.122**	0.281	0.001	0.779	177.856	**0.000**	**0.980**	**-7.895**	**0.328**	< 0.001	329.889	**0.000**	**1.000**	**-5.978**	**0.348**	< 0.001
	HR	-226.229	**0.401**	**0.117**	-0.116	0.000	0.908	200.806	22.950	0.000	-5.615	0.198	< **0.001**	405.483	75.594	0.000	-4.312	0.217	< **0.001**
Fragmentation	Munic.	-226.216	**0.413**	**0.117**	-0.034	0.000	0.908	186.260	8.404	0.015	-7.101	0.283	< **0.001**	396.565	66.676	0.000	-5.514	0.312	< **0.001**
	5 km	-226.327	**0.303**	**0.126**	0.329	0.001	0.743	188.322	10.466	0.005	-6.900	0.271	< **0.001**	397.561	67.672	0.000	-5.386	0.302	< **0.001**
	2.5 km	-226.630	**0.000**	**0.143**	0.634	0.006	0.528	195.288	17.432	0.000	-6.201	0.231	< **0.001**	402.328	72.439	0.000	-4.754	0.252	< **0.001**
	HR	-226.407	**0.223**	**0.130**	-0.431	0.003	0.668	198.739	20.883	0.000	-5.839	0.210	< **0.001**	404.315	74.426	0.000	-4.478	0.230	< **0.001**

Table 5. Set of best performing generalised linear mixed effect models explaining individual predation risk with habitat descriptors, movements and abundance index of roe deer and red fox, with "Family" as a random factor nested in "Area". Most parsimonious model on top of the list; on the bottom we present the null model (i.e. containing the only intercept and random factors).

Model	AIC$_c$	ΔAIC$_c$	ω_i	k
Movements + roe deer abundance + proportion fields 2.5 km	99.849	0.000	0.363	6
Movements + fragmentation 2.5 km + fragm. HR	101.133	1.284	0.191	6
Movements + roe deer abundance + prop. fields HR	101.455	1.606	0.163	6
Movements + roe deer abundance	102.278	2.429	0.108	5
Movements + prop. fields Municipality + prop. fields HR	102.387	2.538	0.102	6
Movements + prop. fields Municipality	103.058	3.209	0.073	5
Null model	131.692	31.843	0.000	3

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Manuscript III

Evaluation of the importance of roe deer fawns in the spring-summer diet of red foxes in southeastern Norway

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Abstract

Even though red foxes *Vulpes vulpes* are the major predators of roe deer *Capreolus capreolus* fawns, it is unclear to what extent the newborn ungulates constitute an important part of the predator's diet. Hence, we conducted a study on the spring-summer diet of red foxes in a fragmented forest / agricultural area in southeastern Norway where a parallel study showed that 25% of the radio-monitored roe deer fawns were killed by the predator annually. Small rodents, especially *Microtus agrestis*, dominated the red fox diet in terms of volume (33%), and medium-large mammals, largely represented by roe deer fawns, constituted the second most important food source (25%). According to our hypothesis, the importance of roe deer in the diet of adult red foxes was highest in early spring, thus supporting previous studies showing that in our study area the predator started actively hunting for the newborn ungulates from the very beginning of the birth season. Contrary to expectations, the occurrence of small rodents in the diet of adult foxes did not increase as their seasonal availability but, on the contrary, significantly decreased, and was replaced during summer by berries and invertebrates. Hence, the summer diet of adult individuals was more diverse than expected at these northern latitudes. The diet of cubs was little diversified, and included a significantly higher proportion of large prey items compared to that of adults. In particular, roe deer remains occurred more frequently in scats found at dens (25%) compared to those from adult foxes (9%), indicating that vixens were using fawns to feed their cubs.Hence, our results suggest that, in areas inhabited by medium density roe deer populations, fawns may be a profitable and significant food source for vixens raising cubs. However, considering the wide food spectrum and the availability of several large prey items in our study area, it appears unlikely that the importance of roe deer fawns to red fox diet and population dynamic could be as great as the impact that the predator has on roe deer populations. This asymmetrical relationship implies that there are unlikely to be any stabilising feedback mechanisms in the predator-prey relationship.

Introduction

Red foxes *Vulpes vulpes* are widely regarded as being one of the most important keystone species within the boreal forest ecosystem of Fennoscandia (Lindström 1989; Lindström et al. 1994; Smedshaug et al. 1999). Within a food web context they are among the species with the greatest number of linkages. Perhaps uniquely among all mammalian predators, they are closely linked to at least three trophic levels, and feed on diverse taxonomic groups. Vegetation, mainly in the form of fruits and berries, is common in their diet in many study areas, as are insects, earthworms, amphibians, small mammals, and birds. Even insectivores are often killed, but less often eaten, and red fox predation on smaller meso-predators has been well documented (Lindström et al. 1995; Palomares and Caro 1999; Linnell and Strand 2000, 2002). What is especially interesting about red foxes is the fact that they also interact with species far larger than themselves – thus linking food webs normally associated with small (stoats *Mustela vision* and weasels *Mustela erminea*), medium (pine martens *Martes martes*, racoon dogs *Nyctereutes procyonoides*) and large predators (wolves *Canis lupus* and lynx *Lynx lynx*). The interaction between red foxes and large predators is complex, as they can be prey (Linnell et al. 1998), vectors for diseases (Degiorgis et al. 2001), or competitors.

Their role as competitors can be both as competitors for the consumable meat of large prey killed by larger carnivores (Selva et al. 2005) and as direct competitors through their impact on shared prey species. This latter effect is most pronounced on the predation impact that red foxes have on roe deer *Capreolus capreolus* fawns. Repeated studies throughout Scandinavia have confirmed that red foxes can kill significant numbers of fawns (Aanes et al. 1998; Jarnemo et al. 2004) and that this predation can elevate neonatal mortality rates above that which is expected in the absence of predation (Andersen and Linnell 1998). From 1995 to 2004 we have studied roe deer fawn survival in southeastern Norway and have found that 62% of fawn mortality is due to red fox predation, and that predation rates vary from 13 to 25% in different study areas (Panzacchi et al. 2007a). Our studies have gone further and tried to understand the complexity of this predator-prey relationship, especially with respect to habitat (Panzacchi et al. 2007b) and alternative prey (Panzacchi et al. 2007c, d) of which earlier studies have indicated the importance (Kjellander and Nordström 2003).

While our roe deer centred studies have indicated the importance of red foxes for the ungulate's population dynamics, the question remains as to whether roe deer fawns are of any real importance for red foxes. The symmetry of the relationship will affect potential feed-back mechanisms and therefore the stability of the predator-prey relationship. Earlier studies on red foxes have indicated that, because of their generalist nature with fluctuating food preferences, in many cases red fox predation may be important for prey even though the prey may be of no real significance for the foxes (Macdonald 1977).

This study aimed to investigate red fox diet during the period when roe deer fawns are available as prey (spring and summer) in a study area where we conducted a parallel study on fawn mortality. In this study site we previously suggested that foxes actually tend to specialise on roe deer fawns and, thus, predation rates are high from the very beginning of the birth season (Panzacchi et al. 2007a). We aimed to test the following predictions. P1: Based on exiting knowledge concerning red foxes in south-central Scandinavia (Lindström 1989 a, b) we predicted that small rodents would dominate red fox diet, and that their occurrence in diet would reflect their seasonal availability. P2: Because red foxes tend to function as temporary specialist predators on roe deer fawns in this study area, we expected that the newborn ungulates would be a major component of fox diet and that their occurrence in diet will be high from the beginning of the birth season. P3: Because of the northern latitude of this study area we expect that invertebrates and plant material would be of minor importance to red fox diet.

Study area

The study was conducted in southeastern Norway, in the counties of Østfold and Akershus (Aurskog-Høland, Enebakk, Høbol, Rælingen, Spydeberg, Trogstad municipalities). The study area consists of a fine mosaic of agricultural land (24%), water (11%) and forest (65%), which is both coniferous and deciduous. During the study period (May-August 2003 and 2004) the average temperature ranged from 10 to 15 °C and 31 to 115 mm rain/month were recorded (Meteorologisk institutt, 2006). The study area is inhabited by relatively large red fox and roe deer populations (Panzacchi et al., 2007a). Among the potential prey for the red fox, the study area is occupied by at least 11 species of voles, mice and shrews (as revealed by a capture mark-recapture study on small mammals, Panzacchi et al. 2007c), moose (*Alces alces*), hares (*Lepus timidus*), *Mustelidae* such as weasel (*Mustela nivialis)* and mink (*Mustela vison*), forest birds such as black grouse (*Tetrao tetrix*) and capercaille (*Tetrao urugallus*), a range of passerines and waterfowl, in addition to domestic sheep, domestic cats and domestic rabbits. Eurasian lynx (*Lynx lynx*) were present in the study area. In accordance to previous studies, which showed that small mammals show multi-annual cycles only approximately above the 60° N (Hanski et al. 1991), in our study area population dynamics are relatively stable (Geir Sonerud, personal communication).

Methods

Collection and analysis of red fox scats

During May-August 2003 and 2004, a total of 171 red fox scats were collected, stored in plastic bags, and frozen at –20°C. Of these, 147 scats were collected by walking 6 transects (1 to 6 km long) previously cleared from old scats, or while carrying out routine radio-tracking of red foxes (Linnell et al., unpublished data). In addition, during summer we visited two dens within the study area and we collected 24 scats representative of the spring-summer diet of red fox cubs. Only apparently fresh scats were collected. Scats analysis was performed by following the methods suggested by Reynolds and Aebischer (1991). Faeces were broken down in water, and microscopic fragments were separated from macroscopic ones using a sieve with mesh size of 0.5 mm. The microscopic residuals were sampled to count earthworms' *chaetae*, while macroscopic fragments were dried and identified by sampling. The discrimination among different *taxa* of medium-large mammals (different species of ungulates, mustelids, insectivores and domestic animals) was done by a microscopic hair analysis of the cuticle, section and medulla using a 400 X microscope (Teerink 1991). The identification of different species of small mammals (mice, voles and rats) was possible only when jaws or teeth were found, and it was done by comparison with reference material. We estimated the number of small mammals in one scat by counting the number of jaws or teeth (Lockie 1959).

Analysis of red fox diet

The red fox diet was analysed using the Frequency of Occurrence (FO), defined as the proportion of scats containing a given food item with respect to the total sample size (Leckie et al., 1998). Even though this is a common way to present results of diet analyses, and it is useful in order to test how often a given food item was ingested, this method is not a good estimator of the nutritional importance of the different prey categories. All methods for extrapolating from occurrence in faeces to biomass or energy consumed are fraught with a range of errors and assumptions (Reynolds and Aebischer 1991). In order to obtain an estimate of the contribution in terms of volume of each prey species, we used the Estimated Ingested

Volume method (EIV) described by Kruuk and Parish (1981), and we categorised the estimated ingested volume of each prey item in each scat into the following categories: < 5%, 6-25%, 26-50%, 51-75%, 76-95%, > 96%. This method has been widely used in meso-predator diet studies (e.g. Lucherini and Crema 1994). However, in order to compare the relative contribution of different prey categories to the estimated total volume ingested, the EIV have been converted into Whole Scat Equivalents, WSE described by Angerbjörn et al. (1999). The WSE is a modified frequency of occurrence calculated with the estimated volume (in our case EIV) of each prey category. For example, one scat with 60% voles and 40% berries plus another scat with 40% voles and 60% berries were considered equivalent to one scat with 100% voles and another with 100% berries. This method has the advantage of maintaining unaltered the same sample size and, thus, allows for a direct comparison of the different proportions ingested. In order to combine FO with volume and, thus, provide a better visualisation of the composition of a typical red fox meal (Fig. 1), we estimated the average volume (AV) of each food item in a scat, defined as the total volume of a given food item in all scats divided by the number of scats containing that food item (e.g. Ciampalini and Lovari 1985).

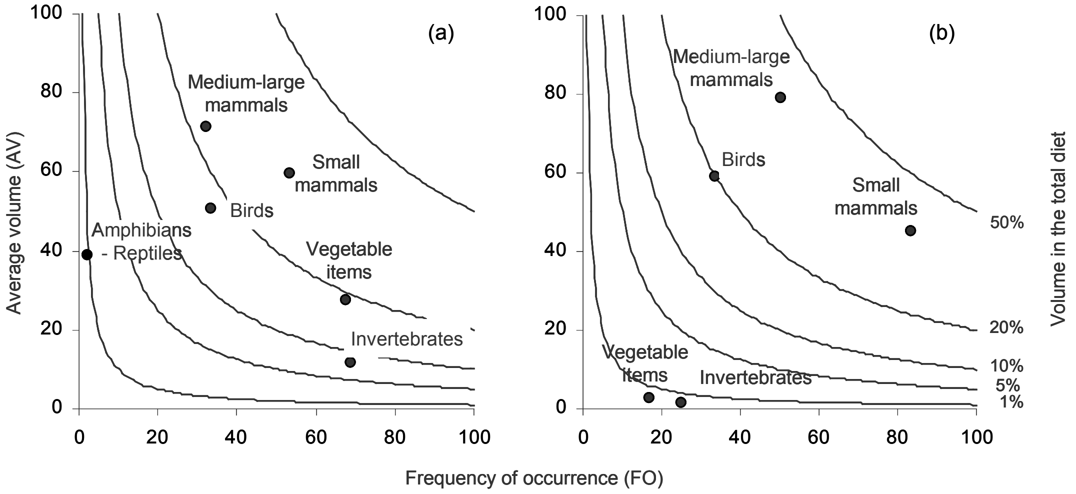

Fig. 1. Representation of the diet of adult red foxes (a) and cubs (b) in south-eastern Norway during May-August 2003 and 2004. Each figure illustrates the relationship between the frequency of occurrence (FO) and the average volume (AV) of the main food items. The isopleths indicate the relative volume of the considered food item with respect to the total volume of all food items. *E.g.*: in (b) the birds occur in 33 % of the scats and account for 60 % of the volume of each of those scats; they represent about 20 % of the volume in the overall spring-summer diet of red fox cubs.

Statistical analyses

In order to assess the feeding habits of adult red fox during the course of spring and summer, we divided the sample in two periods: 15th May – 15th July (n = 51), 16th July – 30th August (n = 96). Differences in FO and WSE were tested by using contingency tables specifying the number of scats where a given food item was present or absent, as suggested by Angerbjörn et al. (1999). The relative importance of different food items was assessed by determining which group gave the major cell contribution to the total χ^2 value in a chi-square test (Dalgaard 2002). Since the proportions of different food items in a scat are interdependent, we tested for variations in the overall diet composition between two periods by applying log-linear likelihood models (G-tests) on contingency tables (Reynolds and Aebischer, 1991).

Logistic regression analyses were performed in order to test for factors affecting the occurrence (presence/absence) of roe deer and small mammals in red fox scats. The category "amphibians - reptiles" was always of insignificant importance in the red fox diet and, thus, it was not included in these analyses. All analyses were conducted by using the statistical software R, version 2.2.1 (R Development Core Team 2006).

Indices of abundance of small mammals and roe deer fawns

Parallel to the study of the red fox diet, two other research projects were carried on during the same period in the study area: a capture-mark-recapture study of small mammals (Panzacchi et al., 2007c), and a study on the mortality of 98 radio-monitored roe deer fawns which took place from 2001 to 2004 (Panzacchi et al., 2007a,b). The index representing the temporal availability of small mammals was calculated as the number of different individuals captured per trap-night during May-August 2003. In order to obtain a reliable estimation of the availability of potential prey for the red fox, we calculated an index of abundance by considering only those species which have been both trapped and found in the scats: *Apodemus* spp. (n = 70), *Clethrionomys* spp. (n = 161) and *Microtus* spp. (n = 98).

The daily availability of vulnerable roe deer fawns was estimated by adopting the method suggested by Mayfield (1975) and Jarnemo et al. (2004). Hence, we calculated the number of roe deer fawns actually alive and radio-monitored every day, corrected according to the red fox preference for different age classes of roe deer fawns. For further details see Panzacchi et al., 2007a, b. Considering that 21 out of 98 fawns captured in the study area were killed by red fox during the first two months of life, that in several cases the carcasses of predated radio-collared fawns were recovered inside fox dens, and that in several cases red foxes had been observed killing or attempting to kill roe deer fawns during the study period, we assume that all roe deer remains detected in the red fox scats belong to the newborn ungulates. Hence, we assume that scavenging on roe deer that had died during winter was finished by May, and that scavenging on roe deer killed by lynx during early summer is insignificant (Linnell J and Teurlings I, unpublished data).

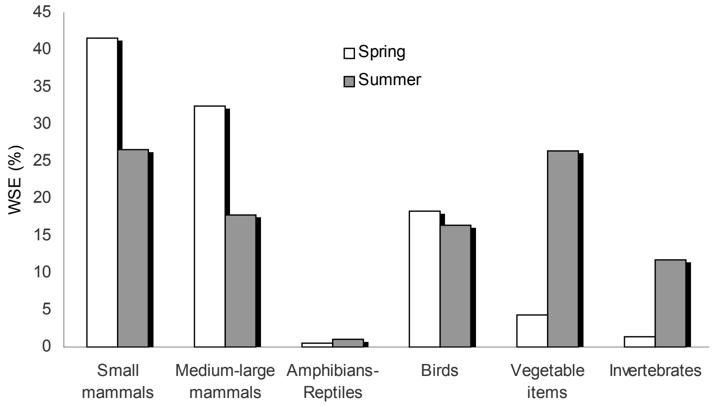

Fig. 2. Whole Scats Equivalents (WSE, in %) of the main categories representing all food items composing the diet of adult red foxes during spring (n = 51) and summer (n = 96) 2003 - 2004.

Table 1. Whole Scat Equivalent (WSE, in percentage) and Frequency of Occurrence (FO) of all food items found in scats from adult red foxes and cubs during May-August 2003 and 2004 in south- eastern Norway.

	WSE (%)					FO				
	Adults			Cubs	Tot	Adults			Cubs	Tot
	Tot	Spr	Sum	Tot		Tot	Spr	Sum	Tot	
Small mammals	31.8	41.6	26.5	37.7	32.6	53.1	60.8	49.0	83.3	57.3
Clethrionomys glareolus	0.7	0.6	0.8	4.2	1.2	1.4	2.0	1.0	0.6	1.8
Clethrionomys rufocanus	0.2	0.0	0.3	0.0	0.2	0.7	0.0	1.0	0.0	0.6
Microtus agrestis	9.6	15.2	6.5	8.5	9.4	17.7	23.5	14.6	16.7	17.5
Arvicola terrestris	5.1	7.8	3.7	12.0	6.1	8.2	11.8	6.3	12.5	8.8
Myopus schisticolor	0.9	0.9	0.8	4.1	1.3	2.0	2.0	2.1	4.2	2.3
Apodemus sylvaticus	0.2	0.7	0.0	0.0	0.2	0.7	2.0	0.0	0.0	0.6
Rattus norvegicus	3.2	1.4	4.1	0.0	2.7	4.1	2.0	5.2	0.0	3.5
Unidentified	11.9	15.1	10.2	8.9	11.5	25.9	31.4	22.9	45.8	28.7
Medium-large mammals	22.9	32.5	17.8	39.5	25.2	32.0	45.1	25.0	50.0	34.5
Capreolus capreolus	6.7	10.1	4.9	20.2	8.6	8.8	11.8	7.3	25.0	11.1
Alces alces	0.7	2.0	0.0	0.0	0.6	1.4	3.9	0.0	0.0	1.2
Mustela vison	1.3	2.0	1.0	0.0	1.2	1.4	2.0	1.0	0.0	1.2
Mustela nivalis	0.7	0.0	1.0	0.0	0.6	0.7	0.0	1.0	0.0	0.6
Sciurus vulgaris	1.6	1.6	1.5	0.0	1.3	2.0	2.0	2.1	0.0	1.8
Lepus timidus	3.0	3.9	2.5	0.0	2.6	3.4	3.9	3.1	0.0	2.9
Erinaceus europeus	0.5	0.0	0.7	0.0	0.4	0.7	0.0	1.0	0.0	0.6
Bats	1.0	1.9	0.5	4.1	1.4	1.4	2.0	1.0	4.2	1.8
Cat	1.7	4.9	0.0	0.0	1.4	2.0	5.9	0.0	0.0	1.8
Sheep	1.5	2.0	1.3	0.0	1.3	2.0	2.0	2.1	0.0	1.8
Pig	0.8	0.4	1.0	11.9	2.4	1.4	2.0	1.0	16.7	3.5
Unidentified	3.5	3.9	3.3	3.3	3.5	6.8	9.8	5.2	4.2	6.4
Birds	17.0	18.2	16.3	19.7	17.4	33.3	35.3	32.3	33.3	33.3
Passeriformes	4.2	6.5	3.0	4.1	4.2	6.8	11.8	4.2	4.2	6.4
Columbiformes	1.5	2.0	1.2	1.3	1.5	2.0	2.0	2.1	4.2	2.3
Galliformes	3.2	2.6	3.6	8.8	4.0	5.4	3.9	6.3	12.5	6.4
Charadriformes	0.4	0.0	0.6	0.0	0.4	0.7	0.0	1.0	0.0	0.6
Falconiformes	0.7	0.0	1.0	0.0	0.6	0.7	0.0	1.0	0.0	0.6
Birds unidentified	6.9	7.0	6.8	5.6	6.7	17.0	15.7	17.7	12.5	16.4
Eggs	0.0	0.1	0.0	0.0	0.0	0.7	2.0	0.0	0.0	0.6
Invertebrates	8.1	1.4	11.7	0.4	7.0	68.7	45.1	81.3	25.0	62.6
Carabus hortensis	0.7	0.2	1.0	0.0	0.6	12.9	5.9	16.7	0.0	11.1
Carabus coriaceus	0.3	0.0	0.4	0.0	0.2	4.1	0.0	6.3	0.0	3.5
Carabus nemoralis	0.2	0.0	0.3	0.0	0.2	1.4	0.0	2.1	0.0	1.2
Carabus violaceus	0.4	0.0	0.6	0.0	0.3	7.5	2.0	10.4	0.0	6.4
Pterosticus sp.	0.8	0.0	1.2	0.0	0.7	11.6	0.0	17.7	0.0	9.9
Geotrupes sp.	2.0	0.7	2.8	0.0	1.8	34.0	19.6	41.7	0.0	29.2
Nicrophorus sp.	0.0	0.0	0.0	0.0	0.0	2.0	2.0	2.1	0.0	1.8
Aphodius sp.	0.1	0.0	0.2	0.0	0.1	1.4	0.0	2.1	0.0	1.2
Coleoptera unidentified	2.2	0.2	3.3	0.1	1.9	32.7	19.6	39.6	16.7	30.4
Hymenoptera	1.2	0.1	1.7	0.0	1.0	8.8	3.9	11.5	0.0	7.6
Anellida	0.1	0.1	0.1	0.1	0.1	7.5	9.8	6.3	8.3	7.6
Others	0.2	0.1	0.2	0.2	0.2	5.4	3.9	6.3	4.2	5.3
Vegetable items	18.7	4.3	26.4	0.5	16.2	67.3	23.5	90.6	16.7	60.2
Berries	16.5	0.9	24.8	0.5	14.3	58.5	7.8	85.4	12.5	52.0
Fruits	0.0	0.0	0.0	0.0	0.0	1.4	2.0	1.0	0.0	1.2
Plants	2.2	3.4	1.6	0.0	1.9	15.0	13.7	15.6	4.2	13.5
Amphibians/Reptiles	0.8	0.5	1.0	0.0	0.7	2.0	2.0	2.1	0.0	1.8
Others/Unidentified	0.7	1.5	0.3	2.1	0.9	6.1	9.8	4.2	4.2	5.8
n	*147*	*51*	*96*	*24*	*171*	*147*	*51*	*96*	*24*	*171*

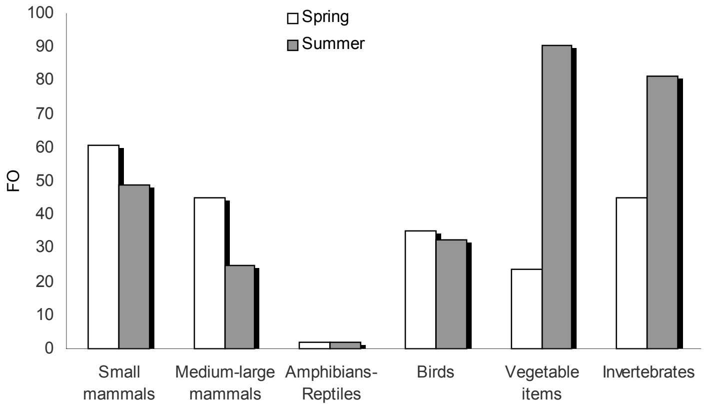

Fig. 3. Frequency of occurrence of the seven categories representing the main food items composing the diet of adult red foxes during spring (n = 51) and summer (n = 96) 2003 - 2004.

Results

Red foxes in our study area had a surprisingly varied diet with 18 species of mammals, 5 bird orders, two species of amphibians and reptiles, plus a wide range of invertebrates, berries, fruits and other vegetation (Table 1). However, the relative contribution of the different food items to the overall red fox diet varied in relation to age class (i.e. adults *vs.* cubs) and season (i.e. spring. *vs.* summer).

Diet of adult red foxes and cubs

Since the diet of adult red foxes did not vary between 2003 and 2004 in terms of estimated ingested volume (WSE: G = 3.400, df = 4, p = 0.493) or frequency of occurrence (FO: G = 1.721, df = 4, p = 0.787), the data were pooled for the analyses. The relative proportion of the main food items to the overall diet of adult foxes was uneven in terms of volume (χ^2 = 28.079, df = 4, p < 0.001). The major contribution to the χ^2 value was given by the category "small mammals", which thus constituted the largest proportion of the diet of adult red foxes during spring and summer (WSE = 32%, Table 1). The field vole *M. agrestis* occurred in the diet more frequently than any other small mammals, but the proportion of the larger-sized *Arvicola terrestris* was also substantial. Medium-large mammals were the second major components of the diet of adult red foxes, and among these roe deer largely dominated. Among birds, *Passeriformes* and *Galliformes* accounted for the main part of the overall spring-summer diet. The relative importance of the main food items in the overall diet of adult red foxes differed not only in terms of ingested volume, but also in frequency of occurrence (χ^2 = 74.059, df = 4, p < 0.001). The category medium-large mammals occurred in the diet less frequently than expected (major contribution to the χ^2 value), while "invertebrates" had the highest FO, occurring in 69% of the scats (2nd major contribution to the χ^2 value).

The overall diet of adult red foxes differed significantly from the diet of cubs at the dens both in terms of volume (WSE: G = 13.930, df = 4, p = 0.008) and frequency of occurrence (G = 22.55, df = 4, p < 0.001). Cubs consumed an overall higher proportion of large prey (mammals and birds) compared to adults (WSE: χ^2 = 6.684, df = 1, p = 0.010). Small mammals (χ^2 = 6.540, df = 1, p = 0.011) and medium-large mammals (χ^2 = 2.223, df = 1, p = 0.136), in particular roe deer (χ^2 = 3.940, df = 1, p = 0.047), were consumed more frequently by cubs than by adult foxes. On the other side, adult red foxes consumed invertebrates (χ^2 = 15.015, df = 1, p < 0.001) and vegetable items (χ^2 = 20.058, df = 1, p < 0.001) more frequently than cubs.

The relative contribution of the various food items to the overall diet of cubs at the dens differed in terms of volume ($\chi^2 = 22.174$, df = 4, $p < 0.001$) and of frequency of occurrence ($\chi^2 = 27.429$, df = 4, $p < 0.001$): vegetable items and insects were underrepresented, while larger prey such as mammals and birds accounted for most of the diet. The relative importance of the main food classes for adult red foxes (a) and for red fox cubs at the dens (b) is illustrated in Fig.1.

Development of the diet of adult red foxes from spring to summer

Fig. 2 and Fig. 3 illustrate, respectively, the WSEs and the FO of the different food items in the diet of adult red foxes during spring and summer. In spring the diet was essentially dominated by small and medium-large mammals, which together accounted for 74% of the WSE. Small mammals represented the most important food item from May to July, accounting for more than 40% of the volume of the total diet ($\chi^2 = 39.500$, df = 4, $p < 0.001$) and occurring in 61% of the scats ($\chi^2 = 15.877$, df = 4, $p = 0.003$). During the same period, medium-large mammals were the second most important food items and, among these, roe deer dominated. Invertebrates and vegetable items were virtually irrelevant in terms of volume. In summer the available food items occurred more evenly in terms of volume, but more unevenly in terms of frequency of occurrence, when compared to spring. However, the overall occurrence of the various food items still differed in terms of volume ($\chi^2 = 10.221$, df = 4, $p = 0.037$), with invertebrates, small mammals and vegetable items dominating the overall food spectrum (Fig. 2). The food items more frequently detected in the scats during summer were vegetable items and invertebrates ($\chi^2 = 132.561$, df = 4, $p < 0.001$).

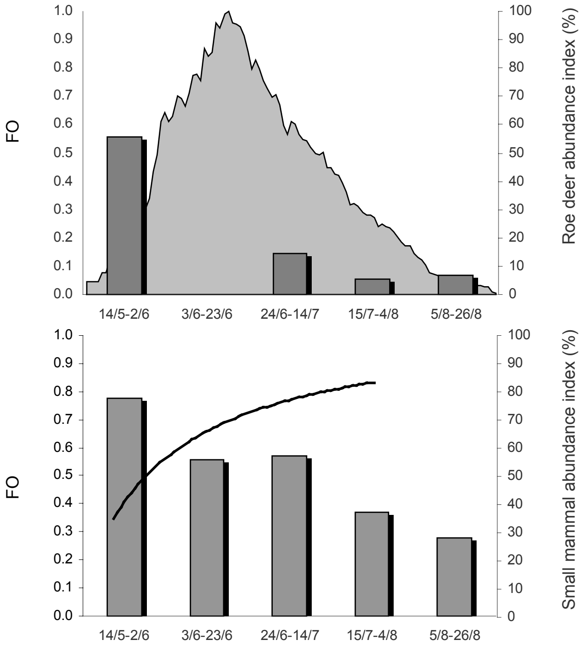

Fig. 4. (a) Frequency of occurrence of roe deer fawns in scats of adult foxes (bars) compared to the index of abundance of roe deer fawns (shaded area) in the stage when they are vulnerable to red fox predation. (b) Frequency of occurrence of small mammals in scats of adult red foxes (bars) during May-August 2003-2004, compared to the index of abundance small mammals (curve) calculated from the 21st of May to the 2nd of August 2003-2004. The indices of abundance are expressed as percentages with respect to the maximum values calculated during spring and summer. The index of abundance and the FO of small mammals refer to: Microtus spp., Chletrionomys spp., Apodemus spp. The indices of abundance of small mammals and of roe deer fawns refer to the same study area where the red fox scats collection has been carried out.

Factors affecting the occurrence of small mammals and roe deer in the diet of adult red foxes

Fig. 4 illustrates the relationship between the index of abundance of roe deer and small mammals and the FO of roe deer and small mammals in the diet of adult red foxes from May to August. During this period, the availability of roe deer fawns reached a peak on the 19th of June and thereafter decreased (Panzacchi et al., 2007a), while the abundance of small mammals constantly increased according to the formula: $y = 30.849 + 2.138\,x /(1 + 0.003\,x)$ (Panzacchi et al., 2007c). Contrary to our expectations, there was no positive relationship between the occurrence of small mammals in scats from adult red foxes and their index of abundance as the season progressed (GLM, $z = 0.432$, $df = 47$, $p = 0.666$). In addition, the occurrence of small mammals in the diet did not increase with time but, actually, decreased ($z = -2.141$, $df = 145$, $p = 0.032$), also when considering only those species for which we have density estimates (*Microtus*, *Clethrionomys* ssp. and *Apodemus*; $z = -2.008$, $df = 145$, $p = 0.045$). The occurrence of roe deer remains in the scats of adult red foxes decreased as summer progressed ($z = -2.443$, $df = 145$, $p = 0.015$) but it was not affected by the index of abundance of roe deer fawns ($z = -0.619$, $df = 145$, $p = 0.536$).

Discussion

The overall picture of red fox diet presented in this study conforms with the surprisingly little data that exists from the boreal forest (mainly Lindström's studies in south-central Sweden; Lindström 1989a,b). The diet was small rodent based (in particular: *M. agrestis*, see also Lindström 1982; O'Mahony et al. 1999), but surprisingly varied for such a northern environment. The results partially supported our predictions P1 and P2, since small rodents were the most important single food item and medium-large mammals, largely represented by roe deer, were the second most important food source in terms of volume. According to our hypothesis (P2), the rapid appearance of roe deer fawns in the diet of adult red foxes right at the start of the season supported previous studies (Panzacchi et al. 2007a) which indicated that, in our study area, the predator really do make an effort to actively hunt for them as they become available in early spring. Considering that during spring some important prey items such as berries are not yet available in the boreal forest, and that the vixens need to re-gain the energy lost during the pregnancy and the lactation period, roe deer fawns may actually be of some importance to red foxes during this critical period. However, during summer the frequency of occurrence of roe deer fawns in the diet of adult foxes markedly declined. Similarly, and partially contrary to our predictions (P2), the frequency of occurrence of small rodents in the diet of adult red foxes did not reflect their seasonal development in availability, but declined significantly as the season progressed. During the course of summer adult red foxes replaced small rodents and roe deer fawns by large amounts of berries and invertebrates. Hence, P3 was rejected, as the summer feeding habits of red foxes were more reminiscent of a Mediterranean diet than one expected from the far north (Calisiti et al. 1990; Lucherini and Crema 1994; Ciampalini and Lovari 1985). In fact it would appear that the most homogenous diets occur at middle latitudes (Jedrzejewski and Jedrzejewska 1992).

The diet of cubs was much less diversified compared the one of adult foxes, and included a significantly higher proportion of large prey items. In particular, roe deer remains occurred more frequently in scats found at dens (25%) compared to those from adult foxes (9%), indicating that vixens were using fawns to feed their cubs. Similar conclusions were proposed by Lindström (1994). Hence, we suggest that as the season progressed and fox cubs started eating solid food, larger prey item were carried to the dens, while adult foxes relied upon other smaller and more easily accessible food sources such as berries and invertebrates. Thus, roe deer fawns may, in some situations, constitute a profitable and relevant food source for red fox cubs (see also Lindström 1994).

However, it should be born in mind that even at the peak of their use, roe deer fawns only constituted on average 10% of the diet of adult foxes and 20% of the diet of cubs. A long-term study in southern Sweden showed that when the population density of voles, which was subjected to marked multi-annual fluctuations, was higher, mortality of roe deer fawns was minimal and vice-versa (Kjellander and Nordström 2003). This suggest that roe deer fawns can represent a key resource whenever their net profitability exceeds that of the main prey item - as it can happen in areas where small rodent populations are cyclic -, or of other alternative large prey items (*i.e.* birds, hares, domestic animals). In our study area the medium-high density of roe deer, which enhanced fawn's profitability (Panzacchi et al., 2007a), induced the predator to use roe deer fawns as a relevant prey item for raising the cubs. However, considering the wide food spectrum and the large availability of medium-large prey, we suggest that roe deer fawns are not an irreplaceable food item for red foxes, and it appears unlikely that the importance of fawns to the diet of foxes, and hence to their population dynamics, could be as great as the impact that the predator has on roe deer populations. Thus, in our study area the newborn ungulates are unlikely to activate any feedback mechanism that could stabilise the predator-prey relationship.

Given that our study area is located in roughly the same climatic zone as Lindström's (1989b) it is unclear what drives red fox abundance, *i.e.* vole density or social regulation. Small rodents in our study area do not demonstrate multi-year fluctuations (Panzacchi et al, 2007c) as they do in Lindström's study area, so it is hard to assess the impact that they have on fox population dynamics. However we believe that, when alternative prey availability is not limited, it is highly unlikely that fawn availability will exert a strong influence on fox reproduction, as they first appear after the critical late winter nutritional bottleneck that determines fox breeding success. In other words, red fox predation on roe deer fawns is an example of an asymmetric relationship where foxes exert a strong influence on roe deer fawns, but fawns probably do not greatly influence red foxes.

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Manuscript IV

Effect of land-use on small mammals' abundance and diversity in a forest-farmland mosaic landscape in south-eastern Norway

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Abstract

Pristine, continuous multi-aged boreal forests of south-eastern Norway have now been converted into patchworks of agricultural areas, clear-cuts and even-aged conifer monocultures, characterised by lower degree of ecological complexity. The effect of these changes on small mammal communities has been much debated. One of the hypothesis states that modern forestry negatively affected both the forest-dwelling *Clethrionomys glareolus*, due to the reduced quality of forests, and open-areas species such as *Microtus agrestis*, due to the rapid development of clear-cuts into forests.

We examined the distribution of several small mammals' species in all available habitat types with respect to both large-scale landscape structure and fine-scale vegetation parameters. Agricultural areas with lowest intensity of use and highest structural heterogeneity - *i.e.* abandoned meadows - supported by far the highest abundance of small mammals, and may thus represent a surplus habitat. The community was clearly dominated by *C. glareolus* in abandoned meadows and by *M. agrestis* in meadows, potentially reflecting inter-specific competition and niche separation. Mature forests and cultivated fields sustained the lowest abundance of small mammals. However, while mature forests also supported the lowest diversity, cultivated fields unexpectedly sustained the highest species richness. Only *Apodemus sylvaticus* reached highest abundance in cultivated fields, but its marked association with edges reflected the need for landscape-scale complexity. Even though *M. agrestis* and *C. glareolus* did not attain highest abundance in clear-cuts and forests, as previously suggested, we found that those patches of clear-cuts or forests characterised by the highest ecological complexity were able to support relatively high abundance of small mammals. In fact, given the high heterogeneity within each habitat type, fine-scale vegetation parameters accounted for a higher proportion of the variance in the species' assemblage (34%) compared to coarse-scale habitat descriptors (29%). In conclusion, our results indicate that agro-ecosystems able to maintain a high degree of fragmentation and heterogeneity – *i.e.* meadows, shelterbelts, and riparian habitats - may provide an opportunity to conserve biodiversity in human-dominated areas. In addition we suggest that, in order to preserve abundant and diverse small mammal communities in human-dominated habitats, landscape planning, forestry and agricultural practices should actively manage for ecological complexity.

Introduction

During the Holocene mature, multi-layered pristine forests, with dead trees and rich substrate, became the most common climax habitat of the boreal and hemi-boreal zones of the northern hemisphere (Stokland *et al.* 2003). Until recently, forest structure and composition were regulated by wild fires, which produced open-structured stands characterised by a deciduous forest phase and structurally complex understory vegetation (Hansson 1992). During the last millennia, most pristine forests worldwide have undergone two major anthropogenic transformations, by being converted into either productive agroecosystems or into timber production stands. Even though human exploitation of virgin forests traces back to the Stone Age, the most radical changes occurred at the end of the 19th century, following the mechanisation of both agricultural (Van Zanden 1991) and timber extraction practices (Stokland *et al.* 2003). Starting from that time, continuous multi-aged boreal forests have been turned into the modern landscape, *i.e.* a patchwork of farmlands, clear-cuts, and dense, fast growing, even-aged conifer monocultures characterised by an overall younger age and by a considerably lower ecological complexity compared to virgin forests (Esseen *et al.* 1992; Hanski 2005; Angelstam, Lindström & Widén 1985).

In recent years, the growing demand for sustainable land management practices has produced a massive amount of literature investigating the impact of either agriculture (Burel *et al.* 2004; Silva, Hartling & Opps 2005) or forestry practises (Hansson 1992; Carey & Johnson 1995; Fitzgibbon 1997; Hayes *et al*. 1997; Bayne & Hobson 1998; Kozaikiewicz *et al.* 1999; Carey & Harrington 2001; Fuller, Harrison & Lachowski 2004; Constantine *et al.* 2004; Sullivan & Sullivan 2006) on a range of species, including small mammal communities, worldwide. The general picture that emerged indicates that clear-cutting and agricultural practices alter species abundance and community structure by favouring open-habitat species such as *Microtus* spp. (Hansson 1978) or forest-field mosaic species such as *Apodemus* spp. (Kozaikiewicz *et al.* 1999) and *Peromyscus* spp. (Pearce & Venier 2005) at the expense of the most common forest-dwelling *Clethrionomys* spp. (Hansson 1978, 1999; Rosenberg, Swindle & Anthony 1994; Sullivan & Sullivan 2001; Pearce & Venier 2005). However, literature provides so many exceptions to this general trend, that the overall picture becomes blurred (see: Wolk & Wolk 1982; Hansson 1978, 1999; Kirkland 1990; Gliwicz & Glowacka 2000; Moses & Boutin 2001; Sullivan & Sullivan 2001; Ecke, Löfgren & Sörlin 2002). A similarly unclear picture appears when considering the relationship between forestry practises and species diversity (Kirkland 1990): while some studies show that old natural forests support higher species diversity than plantations (Saitoh & Nakatsu 1997), others recorded an opposite trend (Sullivan & Sullivan 2001; Constantine *et al*. 2004).

The widespread disagreement on the impact of land use practices on species' diversity and distribution strongly indicates that small mammal communities are affected by factors other than just clear-cutting or agricultural practices per se. Several studies pointed out that the key-factors explaining small mammal abundance and diversity may be habitat complexity and heterogeneity (Carey, Lippke & Sessions 1999, 2001; Ecke *et al*. 2002; Bowman, Forbes & Dilworth 2001; Pearce & Venier 2005). Complex and heterogeneous ecosystems support a higher diversity of ecological niches and, thus, a higher carrying capacity for all members of small mammal communities. However, a clear definition and quantification of complexity and heterogeneity is hard to achieve because of their highly context- and scale-dependent natures. The large majority of the studies investigating the impact of forestry or agriculture on small mammal communities focused on fine-scale aspects of biological-complexity (*e.g.* interaction between woody debris, understory and overstory vegetation) and on the habitat surrounding the study object (see Fitzgibbon 1997; Bayne & Hobson 1998; Bowman *et al*. 2001; Silva *et al*. 2005), but neglected the overall structural complexity at the landscape scale. One risk connected to this approach may be an interpretation of small mammal communities structures biased by an unknown abundance and diversity of species in non-sampled habitat types, which may play a significant, or even a key role in the ecological settings of a given study area.

Nowadays the hemi-boreal region in Scandinavia can be described as a fine-scaled mosaic of cultivated fields, meadows, clear cuts, dense even-aged reforestation blocks and forest stands at the logging maturity age (Angelstam *et al.* 1985; Hansson 1992). Complexity and heterogeneity at the landscape scale are particularly high in south-eastern Norway, where the low density, but widespread, human presence and the small average size of land properties are responsible for much smaller land-management units - as compared to Sweden or America (Esseen *et al.* 1992) -, and for considerable amount of edge habitats. In addition, following the decline in livestock numbers, areas formerly used as grazing or hay meadows have been abandoned and are slowly reverting to forest, thus providing a potentially important habitat in terms of biodiversity (Moen 1998; Staaland, Holand & Kielland-Lund 1998).

To date there have been surprisingly few ecological studies that have attempted to investigate how such a complex landscape structure influences small mammal community structure. In this study we aim to understand how the abundance and diversity of small mammal species varies across the different land-use types associated with this landscape. Based on the most widespread hypotheses concerning small mammal ecology we make the following predictions. P1: That the agricultural habitat types with lowest intensity use and the highest structural heterogeneity (*i.e.* ground cover, bushes and canopy cover), such as abandoned meadows, should support high densities and diversity of species. P2: That the more intensively used, homogenous, croplands should support a low density and diversity of species. P3: Recognising the high variability in vegetation characteristics among each given forest age class, we also predict that fine scaled vegetation characteristics should explain more variation in small mammal community structure than coarse scaled, human-centric, land use categories. (P4) That habitat edges, which provide simultaneous access to different resources, positively affects opportunistic species – *i.e. Apodemus* spp.- and negatively affects the more specialist ones – *i.e. Clethrionomys* spp.

Study area

The study was conducted in May-August 2003 and 2004 in Østfold and Akershus counties, south-eastern Norway. In order to strengthen the outcomes of our study and to obtain results unbiased by the peculiarities of a given study site, small mammals' trapping was carried out alternatively in two distinct areas, characterised by a very similar landscape structure and composition, approximately 30 km apart. The study area is made up of a fine mosaic of agricultural areas (*i.e.* cultivated fields, meadows and abandoned meadows; 30%), lakes and rivers (12%) and intensively managed even-aged forest plots (58%), for the most part coniferous (Norwegian spruce *Picea abies*, and Scots pine *Pinus sylvestris*) with scattered patches of birch (*Betula spp.*) and other deciduous trees. Pristine forests are virtually absent from the study area, and the oldest forests are those at "logging maturity" (*i.e.* ready to be harvested; Stokland *et al.* 2003). The study area lies in the hemi-boreal biogeographical zone, characterised by milder climatic conditions compared to the neighbouring boreal region. According to the Norwegian Metereologic Insititute (2006), during the study period - from the end of May to the beginning of August each year - the average precipitation was 4.7 mm/day, and the average temperature was 16·3 °C. In accordance to previous studies, which showed that small mammals show multi-annual cycles only above the 60° N (Hanski, Hansson & Henttonen 1991), in our study area population dynamics are relatively stable (Geir Sonerud, personal communication).

Table 1. Description of the parameters used for the analyses. Land use descriptors and vegetation descriptors were recorded within the perimeter of each small quadrate - SQ (15 x 15 m). For most of the vegetation parameters we recorded the percentage cover and the average height (height) within the SQ.

	Parameter	Description
Habitat type	Clear-cut	
	Young forest	Young plantation and pole sized stands*
	Mature forest	Medium aged stands and mature stands*
	Crop	Cultivated fields
	Meadow	Grassy, uncultivated areas, never with livestock grazing
	Abandoned meadow	Unmanaged meadows with sparse trees and bushes
Vegetation descriptors	N trees	N of trees within SQ. 1-10, 10-20, 20-30, 30-40, > 40
	Tree height	
	Moss percentage / height	
	Herb percentage / height	Herbaceous plants
	Crop	Cultivated cereals and rapeseed; present/absent
	Crop height	
	S berry percentage / height	Small berries: mostly blueberry and cowberry
	T berry percentage / height	Tall berries: mostly raspberry
	Bush percentage / height	Woody plants < 1·5 m, berries excluded
	Woody debris percentage / height	Dead tree trunks, branches and woody fragments
Proximity to edges	Edge	Closest neighbouring habitat type
	Distance	Distance to the closest neighbouring habitat type
Other	Date	Week number
	Rain	Average daily precipitation (mm) per trapping period **
	Area	Sub-area

*According to Børset 1985

**Norwegian Meteorological Institute (2006); data from the weather station closest to the study area

Methods

Trapping method

Small mammals were trapped using Ugglan Special multi-capture live-traps (Hansson 1994), designed for capturing shrews, mice and voles. Each individual - except from shrews - was marked by clipping a small spot of fur on its back before being released. Each trap was provided with a metal roof and with a polystyrene mat in order to maximise survival probabilities in every weather conditions. Traps were baited with a diverse menu - green apples, yarns soaked in peanut butter, and wheat grains - in order to attract both vegetarian and omnivore species. Small mammals were trapped each year during 5 trapping sessions lasting 10 consecutive days each, for a total of 100 trapping days in two years. The traps were organised in small quadrates (SQs, Myllmäki *et al.* 1971), which are 15 x 15 m trapping units composed of 12 traps evenly positioned along the perimeter. The SQs were distributed in six habitat types (Table 1). Since the "abandoned meadow" habitat type was only introduced during mid-way through the first year trapping sessions, we had to correct for the sample size. Hence, in 2003 we used 240 traps divided into (a) four SQs in each of the first five habitat types described in Table 1 during the trapping sessions 1st - 4th; (b) two SQs in each of these habitat types and ten SQs in abandoned meadows in the 5th session. The following year we sampled equally each habitat type by dividing 216 traps into 3 SQs per habitat type during each trapping session. Within the perimeter of each SQ we recorded 16 vegetation parameters (Table 1). Other variables used in the analyses are described in Table 1. All traps were checked every morning for 10 consecutive days, and then moved to another area.

Table 2. Number of small mammals captured in 2280 night/traps during May-August 2003 and 2004 in south-eastern Norway, divided per species and habitat type; the last two columns summarise the total number of captures and recaptures.

Latin name	Common name	Mature forest	Young forest	Clear-cut	Crop	Meadow	Abandoned meadow *	TOT	
								Capture	Recapture
Clethrionomys glareolus	Bank vole	51	69	46	4	36	112	318	692
Clethrionomys rufocanus	Grey-sided vole	8	7	6	0	0	4	25	59
Microtus agrestis	Field vole	0	8	33	16	118	48	223	352
Apodemus sylvaticus	Wood mouse	7	9	3	50	12	15	96	143
Apodemus flavicollis	Yellow-necked mouse	0	0	1	6	0	1	8	18
Mus musculus	House mouse	0	0	0	2	0	0	2	1
Sorex araneus	Common shrew	22	92	95	5	73	150	437	**
Sorex minutus	Pygmy shrew	0	2	0	2	0	1	5	**
Neomys fodiens	Water shrew	0	1	1	0	0	0	2	**
Myopus shisticolor	Wood lemming	0	0	0	1	0	0	1	**
Arvicola terrestris	European water vole	0	0	1	0	3	0	4	0
TOT		88	188	186	86	242	251	1121	1266

* Corrected according to the lower number of small quadrates in abandoned meadows (25) compared to all other habitat types (33)
** Not marked at capture

Estimation of population size

The population size for each of the more common small rodent species in the six coarse-scale habitat types was estimated by considering the trapping history of each individual by means of a capture-mark-recapture analysis performed with the program *MARK 4.3* (White & Burnham 1999). We assumed that during each 10-day trapping session the population was closed and, thus, we selected the "closed capture" analyses (Otis *et al*. 1978). These models are based on the full likelihood parameterisation with three types of parameters: p_i, probability of first capture; c_i, probability of recapture, and N, the abundance. For each species, we ran different models: M_0, which assumes equal capture probability for all animals on all trapping occasions; M_b, which assumes different capture and recapture probabilities; M_t, which assumes that capture probabilities vary with time. We selected the most parsimonious model by using the Akaike Information Criterion corrected for small samples (AIC_c), following Burnham & Anderson (2002).

Analysis of the relationship between species and environment

The relationship between small mammals abundance and environmental variables was investigated both separately for each of the three most common species, and for the overall small rodents community. Shrews were excluded from these analyses because they are strictly insectivorous and, thus, only indirectly associated with the considered environmental variables.

For the first part of the analyses, we used principal component analysis, PCA (Jongman, ter Braak & van Tongeren 1995), to reduce the parameters describing the percentage vegetation cover, which were correlated, to a few principal components (Table 3). Only components that explained more than 10% of the variance among vegetation variables were considered. Before we performed the PCA, all variables were scaled according to Becker, Chambers & Wilks (1988). Proportion data were arcsine - square root transformed following (Zar 1984). In order to identify the best model describing the abundance of each of the three most common species, we performed generalised linear models by considering the number of different individuals captured during 10 days in each SQ - also known as the minimum number known to have been alive - as the dependent variable, and assuming a negative binomial distribution, which is commonly used to describe the distribution of count data in which the variance is greater than the mean (Crawley 2002).

For the analysis of the relationship between environmental variables and small mammal community we chose ordination methods. At first we inspected the general structure of the data regarding the different species of small rodents by using a detrended correspondence analysis, DCA (Hill 1974; Hill & Gauch 1980). Since the length of the first axis described by the DCA was below 3 standard deviation units, we adopted a linear response model, as recommended by ter Braak & Prentice (1988) and ter Braak (1995). Rare species were down-weighted. Then, in order to determine the major patterns of variation in the species' assemblage that was explained by our environmental variables, we performed a stepwise redundancy analysis, RDA (Rao 1964). This constrained ordination method selects the linear combination of environmental variables giving the smallest total residual sum of squares, and uses it to explain the variation in species composition (ter Braak 1995). The environmental variables shown in the plots were selected by performing permutation tests between species composition and one environmental variable at time. Monte Carlo permutation tests (ter Braak 1992) were used to test for the significance of the relationship between species distribution and environmental variables (999 permutations). The analyses were performed using the *R 2.2.1* (R Development Core Team 2005) software; the RDA analysis was performed using the *Vegan* package (Oksanen, Kindt & O'Hara 2005).

Table 3. Selection of the most parsimonious models describing the population size of the three most common small rodent species based on capture and recapture probabilities. Each model was built on different assumptions: M_0, similar capture and recapture probabilities; M_t, same as M_0, but probabilities vary with time; M_b, capture and recapture probabilities differ. Models are ranked by the AIC_c, and the most parsimonious model for each species is reported in the first raw; *k* = number of parameters, ω_i = Akaike's weights, *i.e.* normalised likelihood of the models.

Species	Model selection				
	Model	AICc	ΔAIC_c	ω_i	*k*
Clethrionomys glareolus	M_b	1541·20	0·00	1·00	8
	M_0	1655·86	114·64	0·00	6
	M_t	-	-	-	-
Microtus agrestis	M_t	832·28	0·00	0·99	15
	M_b	844·63	12·34	0·01	7
	M_0	912·46	80·17	0·00	6
Apodemus sylvaticus	M_b	554·83	0·00	0·79	8
	M_0	557·82	2·99	0·18	6
	M_t	561·37	6·54	0·03	15

Diversity indices

Species diversity was estimated by the combination of the index of species richness and PIE Hurlbert´s (1971) index of species evenness, calculated using the *Ecosim 7.69* software (Gotelli & Entsminger 2006). Since the estimated richness is strongly dependent on the sample size (*i.e.* the number of specimens in the community), in order to compare samples of different size, it is necessary to calculate their expected richness at standardized size. This can be done through rarefaction analyses (Olszewski 2004). For example, if community A has 500 individuals belonging to 40 species and community B has 250 individuals belonging to 30 species, rarefaction analysis provides the expected number of species to be found in a sample of 250 individuals randomly drawn from community A, thus allowing for a direct comparison between the species diversity in communities A and B (Gotelli & Entsminger 2006). Hence, for each habitat type we performed a 1000 iterative simulations by randomly sub-sampling a growing number of individuals and, in order to rank the diversity indices in different habitat types, we standardised the sample sizes according to the habitat type with the lowest number of individuals.

Table 4. Results of the principal component analysis, PCA, of the vegetation descriptors. An interpretation of the principal components (PCs) is provided, based on the highest variable loadings for each variable. Continuous variables have been scaled, and those describing the proportion of cover have been arcsine - square root transformed.

		PC1	PC2	PC3
	Interpretation of PCs	Late successional traits	Ground cover complexity	Berry-rich clearings
Loadings	Tree height	-0·535		
	N trees	-0·430	0·119	
	Moss percentage	-0·441	0·170	
	Herb percentage	0·143	0·609	-0·400
	Crop	0·284	-0·597	-0·148
	Bush percentage		0·412	0·232
	Small berry percentage	-0·472	-0·112	
	Tall berry percentage		0·198	0·514
	Woody debris percentage			0·695
Importance of components				
	Standard deviation	1·686	1·294	1·100
	Proportion of variance	0·316	0·186	0·135
	Cumulative proportion	0·316	0·502	0·636

Results

During the course of the study, 1121 individual small mammals, belonging to 11 different species, were trapped (Table 2). The low number of water voles captured may be due to the relatively small size of the traps, which were not designed for capturing this species. Mortality never occurred for *Apodemus* spp., and varied between 0% and 1% for *Microtus agrestis* and *Clethrionomys* spp; on the contrary, due to their high metabolism, most of the shrews died in the traps. The following non-target species were captured, and released alive: 8 lizards, 2 toads, 3 frogs, 3 weasels; in 3 cases a field vole gave birth inside the trap to 5-6 live offspring.

Population estimate

The capture-mark recapture analyses (Table 3) indicated that the population sizes of different species were best estimated by using models based on different assumptions. For bank voles and wood mice the most parsimonious model (M_b) assumed different capture and recapture probabilities. In particular, for both species capture probability (0·111 ± 0·018, and 0·129 ± 0·030, respectively) was much lower than recapture probability (0·343 ± 0·012; 0·222 ± 0·019). For field voles the best model (M_t) assumed that capture and recapture probabilities increased with time during the 10-days trapping period.

Table 5. Set of generalised linear models explaining the index of abundance of the most common small mammals captured with vegetation descriptors, represented by the PCs (Table 4), and with other variables (Area, Date, Rain, Edges and Distance) described in Table 1. Models were ranked according to the AICc, with the most parsimonious model on top of each list.

Species	Model	AIC_c	ΔAIC_c	ω_i	k
Clethrionomys glareolus					
	PC1 + PC2 + PC3 + Edge + Date	598·32	0·00	0·45	10
	PC1 + PC2 + PC3 + Edge + Date + Area	599·78	1·46	0·22	11
	PC1 + PC2 + PC3 + Edge + Date + Rain	600·28	1·96	0·17	11
	PC1 + PC2 + Edge + Date	600·48	2·16	0·15	9
Microtus agrestis					
	PC1 + PC2 + PC 3 + Edge + Date + Area	431·67	0·00	0·43	11
	PC1 + PC2 + PC3 + Edge + Date + Area + Rain	432·93	1·26	0·23	12
	PC1 + PC2 + PC3 + Edge + Date	433·22	1·55	0·19	10
	PC1 + PC2 + PC3 + Edge + Date + Distance + Area	433·88	2·21	0·14	12
Apodemus sylvaticus					
	PC1 + PC2 + Edge + Date + Area - Rain	300·40	0·00	0·32	11
	PC1 + PC2 + Edge + Distance + Date + Area + Rain	300·51	0·11	0·30	12
	PC1 + Edge + Distance+ Date + Area + Rain	300·80	0·40	0·26	11
	PC1 + PC2 + PC3 + Edge + Distance + Date + Area + Rain	302·40	2·00	0·12	12

The estimated population size of each of the three species differed among the six habitat types (Fig. 1): bank voles were more abundant in abandoned meadows and less abundant in crops (χ^2 = 178·842, df = 5, $P <$ 0·001); field voles thrived in meadows and avoided mature forests (χ^2 = 275·593, $P <$ 0·001); wood mice preferred crops and avoided clear-cuts (χ^2 = 126·661, $P <$ 0·001). In total, the population estimates for the three species calculated within the perimeter of the SQs differed among habitat types (χ^2 = 140·802, $P <$ 0·001), being highest in abandoned meadows and meadows, and lowest in mature forests.

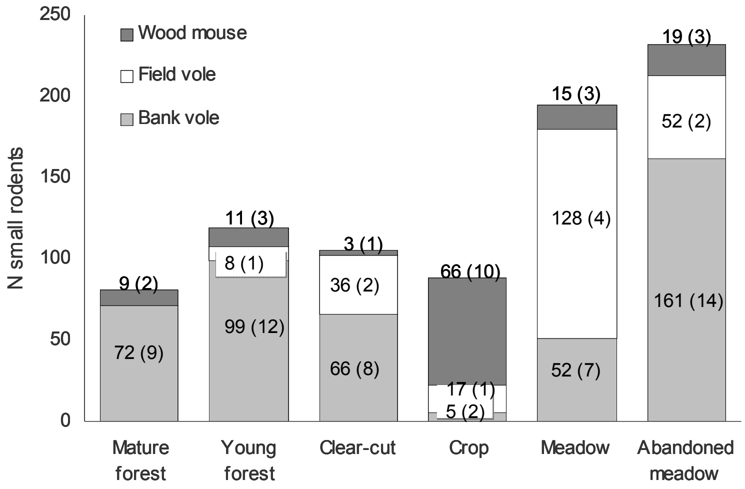

Fig. 1. Population estimates (S.E. on the brackets) for the most frequently trapped small rodents (*Clethrionomys glareolus, Microtus agrestis, Apodemus sylvaticus*) calculated by the capture-mark-recapture analysis, inside the small quadrates (SQ) located in each habitat type. The population estimates in the abandoned meadow were corrected according to the lower number of small quadrates in this habitat type (n = 25) compared to all other habitat types (n = 33).

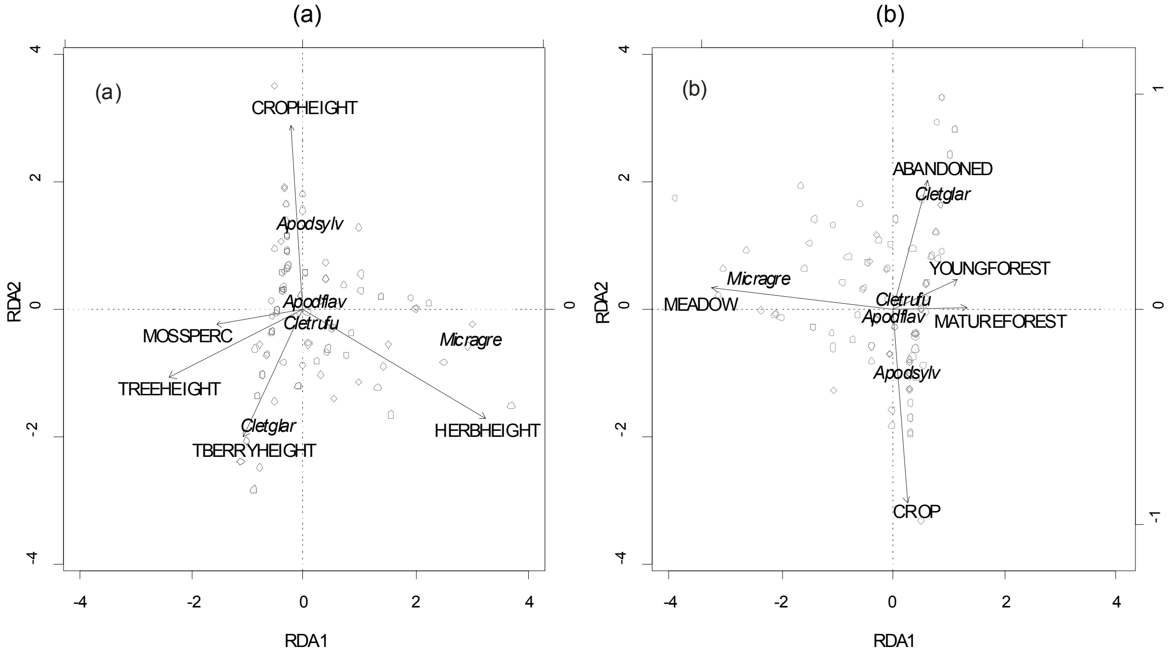

Fig. 2. Biplots of (a) vegetation – RDA and (b) habitat - RDA. Relationship between vegetation parameters (a) and habitat types (b), and the 5 most frequently trapped small rodents' species as determined by stepwise redundancy analysis. The length and direction of each vector is proportional to the strength of the association between the environmental variables within each plot and the RDA axes. For abbreviations see Table 1, 2.

Factors affecting species abundance

Nine variables describing the proportion of ground cover were reduced to three principal components, which explained 64% of the variance in the data set (Table 4). The first component (PC1) was negatively correlated with the number and height of trees, and with the proportion of moss and small berries. Therefore, PC1 can be interpreted as a factor related to late successional stages; PC2 was positively correlated with the proportion of non-cultivated herbaceous vegetation and bushes, and can be interpreted as a factor related to the complexity of the ground cover; PC3 was positively correlated with the proportion of woody debris and tall berries and, thus, it was related to old, productive clearings colonised by raspberries.

The most parsimonious model explaining the abundance of bank voles included all three principal components, indicating a positive relationship with old mossy forests rich in blueberries (PC1, $P < 0{\cdot}001$), with the complexity of the ground cover (PC2, $P < 0{\cdot}001$), and with raspberry-rich clearings (PC3, $P = 0{\cdot}058$). The type of habitat at the edge was also included in the best model, and bank voles were negatively affected by the proximity of young ($P = 0{\cdot}076$) or mature forests ($P = 0{\cdot}026$). In addition the abundance of bank voles increased as summer progressed ($P = 0{\cdot}020$). The abundance of field voles also increased with time ($P = 0{\cdot}003$), and was affected positively by the complexity of the ground cover (PC2, $P < 0{\cdot}001$), and negatively by late successional stages (PC1, $P < 0{\cdot}001$) and woody debris (PC3, $P = 0{\cdot}037$). In addition, the abundance increased in the northern sub-area ($P < 0{\cdot}001$) and was higher when the neighbouring habitats were meadows ($P = 0{\cdot}026$), abandoned meadows ($P = 0{\cdot}002$), crops ($P = 0{\cdot}004$) or old forests ($P = 0{\cdot}003$), but not clear-cuts ($P < 0{\cdot}001$). The wood mouse, on the contrary, was more abundant in the southern sub-area ($P = 0{\cdot}054$) and decreased as the season progressed ($P = 0{\cdot}011$), as the species typically exhibit annual population cycles with lowest densities in summer (Tattersall *et al.* 2004). As expected, wood mice were also positively affected by the proximity of meadows ($P = 0{\cdot}060$) and cultivated fields ($P = 0{\cdot}078$), and were correlated positively to crops (PC2, $P = 0{\cdot}032$) and negatively to older successional stages (PC1, $P = 0{\cdot}007$). During rainy weeks, the probability of trapping wood mice was lower ($P = 0{\cdot}029$).

Factors affecting community structure

The DCA-plot of species revealed that the yellow-necked mouse was distant from the other small rodent species. Since this would affect the gradient length and since this species occurred in low numbers, we decided to exclude it from the DCA. The DCA gradient length was then 2·8 and therefore a linear response model was chosen (ter Braak & Prentice 1988; ter Braak 1995). We explained the variation in small rodents assemblage in two separate RDA analyses: one by using vegetation parameters (vegetation-RDA, Table 6a) and the other by using habitat types (habitat-RDA; Table 6b) as constraining variables. By dividing the constrained inertia (the sum of all canonical eigen values) for the total inertia (a measure of the total amount of variance in a data set) it is possible to find how much of the variance in species' assemblage is accounted for by the selected combination of environmental variables. Therefore, the vegetation variables accounted for 34% of the variation in the assemblage (Table. 6a). Permutation tests showed that the vegetation parameters explained a significant amount of the variance in species' assemblage (*Pseudo-F* = 0·528, P < 0·001). Field voles showed affinity with herbs height and negative correlation with tree height, while wood mice showed affinity to crops height. Bank voles correlated positively with berry height, while yellow-necked mice and grey-sided voles didn't show affinity with any of the environmental variables (Fig. 2a).

Habitat types (Table 6b) explained 29% of the variation in species' assemblage, and the permutation test showed that the selected variables explained a significant amount of the species' variation (*Pseudo-F* = 0·403, P < 0·001; Table 6b). Field voles showed affinity with meadows and negative correlation with both old and young forest, while wood mice showed affinity to crops. Bank voles correlated positively with abandoned meadows, while yellow-necked mice and grey-sided voles didn't show affinity with any of the habitat types (Fig. 2b).

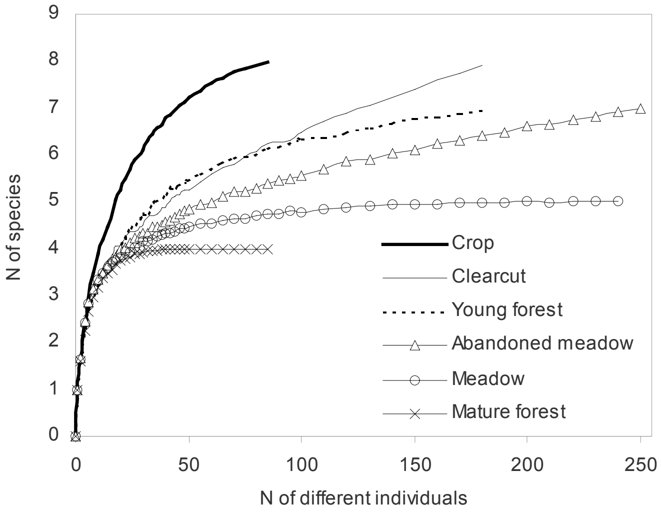

Fig. 3. Rarefaction curves illustrating how species richness increases with the number of captures within each habitat type. Each curve has been constructed by performing 1000-iteration simulation by randomly sub-sampling a growing number of individuals within each habitat type.

Biodiversity

In Fig. 3 we present rarefaction curves for species richness in each habitat type. A clear asymptote was reached only by mature forests and meadows, indicating that a further sampling in these habitat types would not have revealed a higher species diversity than we observed. On the contrary, species richness may have increased with a higher sampling effort in the other habitat types. The figure shows that the highest species richness was recorded in crops, and the lowest in mature forests. However, the comparison of the 95% confidence intervals of the diversity indices standardised for equal sample size (Table 7) indicates that the species richness did not significantly differ between crops and clear-cuts, while it was significantly lower in mature forests compared to young forests. Species evenness reached the highest values in abandoned meadows, but the difference was significant only when compared to mature forests, which supported the lowest relative distribution of individuals among species.

Discussion

The landscape approach adopted in our study design allowed us to obtain a clear picture of the relative distribution of small mammal species in relation to all available non-urban habitat types in an area representative of south-eastern Norway. In addition, the study of the relationship between fine-scale habitat descriptors and small mammal abundance allowed us to control for the wide environmental heterogeneity within each habitat category, and improve the understanding of the overriding factors affecting species abundance and distribution.

As predicted (P1) abandoned meadows alone supported the highest abundance of small mammals, both when considering the minimum number of individuals alive belonging to all trapped species (Table 2) and the more accurate population estimates for the three most common species (Fig. 1). Even though the availability of this habitat type was negligible from a landscape perspective, abandoned meadows may constitute a surplus habitat (sensu Hansson 2002) for the two most common species - bank voles and common shrews - and, together with meadows, play a key-role for the overall small mammal community. Notwithstanding the close similarity between these two habitat types, small mammal communities were clearly dominated by bank voles in abandoned meadows and by field voles in meadows, potentially reflecting both inter-specific competition (Huitu, Norrdahl & Korpimäki 2004), and the partial trophic niche separation between the two species - bank voles being a mixed granivorous-folivorous species (Hansson 1999) in contrast to field voles that prefer grass stems (Hansson 1971). Wood mice which, typically, showed marked preferences for agricultural lands (Tattersall *et al.* 2002), still attained high densities in meadows and abandoned meadows, or benefited from their proximity. According to P4, the more opportunistic species – wood mice, but also field voles – were positively affected by the proximity of habitat edges, while bank voles were negatively affected by habitat fragmentation.

Not only did abandoned meadows supported the highest species evenness, but also the rarefaction curve, illustrating the increase in number of species with the sample size (Fig. 3), attained high values without reaching an asymptote, thus indicating a good potential also in terms of species richness. Interestingly, abandoned meadows supported both a higher overall abundance and diversity of small mammals compared to their more intensively exploited twin habitat, *i.e.* meadows. Semi-natural grasslands are well known for being one of the richest habitats in terms of plant species in northern Europe (Rosef & Bele 2005), and the availability of potential ecological niches for small mammals supported by the vegetational complexity of this habitat type (*i.e.* pre-interactive niche diversification; Carey & Harrington 2001) may account for part of the observed high diversity and abundance of small mammals.

None of the species studied reached highest densities in either clear-cuts or young forests, although the overall abundance of small mammals supported by these habitats was not negligible. However, the analysis of fine-scale habitat descriptors revealed that PC3 - interpreted as raspberry-rich clearings - was negatively correlated to field voles' abundance, and was not relevant at all for wood mice (Table 5). Bank voles were, actually, positively affected by PC3, but this fact alone did not allow us to distinguish between a positive effect of woody debris and / or raspberry (Table 4). The redundancy analysis clarified this issue by showing that bank voles were strongly associated with the presence of raspberry, but neither the proportion of woody debris (Fig. 2a) and the "clear-cut" habitat type (Fig. 2b) were included among the relevant variables describing the species' distribution. Hence, we deduced that only clear-cuts with a relatively high degree of structural complexity and productivity (*i.e.* colonised by raspberry bushes) were able to support abundant bank vole populations. Similar conclusions can be reached regarding young forests and mature forests. While field voles and wood mice virtually avoided them, bank voles attained relatively high densities in both habitat types. However, given the strong positive association with both late successional traits (tall trees, moss and blueberries - PC1) and ground cover complexity (PC2), and the lack of association with young forest or mature forest in the habitat - RDA (Fig. 2b), it seems likely that the relatively high abundance reached in some of the plots located in these habitat types was more related to fine-scale ecological characteristics rather than to the forest age class *per se* (Table 1, 5, Fig. 2). Hence, in accordance with P3, fine-scale vegetation parameters accounted for a considerably higher proportion of the variance in the overall species' assemblage (34%, Fig. 2a) compared to coarse-scale habitat descriptors (29%; Fig. 2b).

Quite significant was the fact that we did not detect dense populations of field voles on clear cuts, as there has been much speculation in Scandinavia that clear-cutting has greatly altered small mammal communities by favouring this species (Ims 1991). In fact our study found higher densities of the so-called "mature forest specialist" bank voles, compared to field voles, on clear cuts.

Mature forests and cultivated fields sustained the lowest abundance of small mammals compared to all other available habitats. However, while mature managed forests supported also the lowest species diversity, further lowering the importance of this habitat type for small mammal communities, cultivated fields unexpectedly sustained the highest species richness recorded in this study (in contrast to P2). It is widely accepted that the intensification and expansion of modern agriculture is amongst the greatest current threats to biodiversity worldwide (Pimentel *et al.* 1992; Hanski 2005; Hole *et al.* 2005; Michel, Burel & Butet 2006). However, agroecosystems that maintain a high degree of structural complexity – *e.g.* shelterbelts, riparian zones, interspersed woodlots and an overall spatial heterogeneity – may provide an opportunity to conserve biodiversity in human-dominated areas (Paoletti *et al.* 1992; Bignal & McCracken 1996). This could be the case for agroecosystems in south-eastern Norway, which are embedded in a matrix of forested areas and semi-natural grasslands and still have the potential to attract, even though only occasionally, several generalist species. However, these artificial ecosystems may be unable to sustain entire small mammal communities. Only one species - the wood mouse - reached high densities in this habitat type (see also Hansson 2002; Tattersall *et al.* 2002, 2004), but its marked association with field margins reflected a clear need for a certain degree of ecological complexity at the landscape scale (see also Hansson 1994; Bayne & Hobson 1998). It is difficult to establish whether the sporadic presence of species other than wood mice in cultivated fields could be interpreted as a spill-over effect from -surplus areas such as meadows and abandoned meadows, which sometimes - but not necessarily - were close to agricultural areas. Furthermore, the fact that most cultivated fields are ploughed in the autumn in this study area imply that the year round persistence of these species may depend on the close proximity of other habitats that provide suitable winter habitat (Todd *et al.*, 2000; Tattersall *et al.* 2004).

In agreement with several authors (Carey *et al.* 1999, Carey & Harrington 2001; Bowman *et al.* 2001; Ecke *et al.* 2002; Pearce & Venier 2005) our results support the hypothesis that fine-scale vegetational diversity is a key-factor determining the impact of forestry on small mammal communities at different spatial scales. We suggest that, irrespective of the forestry practice, each species would reach higher abundance in those coarse-scale habitat types providing - at a given time and place - the species' ecological requirements in terms of cover, food and inter-specific relationships. Hence, in accordance with Kerr & Packer (1997), we suggest that heterogeneous landscapes offering a higher availability of pre-interactive ecological niches have a higher potential in terms of biodiversity compared to homogeneous landscapes. A similar argument can be proposed at a smaller spatial-scale, with more heterogeneous habitat types in terms of vegetational parameters supporting a higher species diversity (Sullivan & Sullivan 2006). An exception is represented by crops [CROP] , which, notwithstanding the ecological over-simplification, provide artificially selected high-quality food and, in some circumstances, may represent an occasionally attractive habitat type for different species. It should be clearly stated, however, that we are discussing biodiversity within human-altered ecosystems, which are known to favour opportunistic species at the expenses of those specialised to the lost ecological complexity of pristine forests (Hanski 2005).

Considering even smaller spatial scales - within the preferred coarse-scale habitat types - we suggest that each species would reach the highest abundance in those patches offering the highest fine-scale vegetational complexity. Accordingly, several authors described clear temporal variations in the response of small mammals communities to clear-cutting practices, possibly related to variations in the ecological complexity of the re-developing successional stages (Moses & Boutin 2001; Pearce & Venier 2005).

Several authors have reported a long-term decline in *Clethrionomys* spp. and *M. agrestis* in northern Scandinavia. One of the most mentioned factors possibly related to this decline is modern forestry which, on one side reduces the forest quality for *Clethrionomys* spp., and on the other favours a rapid development of clear-cuts into forests, thus negatively affecting open-areas species like field voles (Hanski *et al.* 1993; Hansson 1999; Hörnfeldt 2004). Unfortunately, no data are available on long-term vole population dynamics in our study area, but our data do indicate that bank voles are able to do well in a wide range of forestry age classes and agricultural habitat types. However, based on our results we suggest that the availability of suitable habitats other than fast-growing clear-cuts and impoverished managed forests (*i.e.* meadows, abandoned meadows and crops) in south-eastern Norway might have mitigated the negative impact of forestry practices on vole populations by providing alternative areas of expansion. Furthermore, in purely forested landscapes forestry practices are supposed to partially force bank voles to occupy clear-cuts, where field voles thrive and, due to their relaxed social system, are able to reach higher densities compared to the territorial bank voles (Hanski *et al.* 1993; Hansson 1999). On the contrary, the higher availability of suitable habitat types in south-eastern Norway allow for a clear landscape-scale niche separation, thus avoiding a direct competition between bank voles and field voles (Huitu *et al.* 2004).

In conclusion, we suggest that the general disagreement about the effect of forestry or agricultural practices on small mammal communities (see Ecke *et al.* 2002) may be due to differences in the impact of management practices on the ecological complexity of the habitat at both the overall landscape scale and at the detailed vegetation scale at each given time and place. However, according to Carey *et al.* (1999), in order to preserve abundant and diverse small mammal communities in human-dominated habitats, landscape planning, forestry and agricultural practices should actively manage for ecological complexity.

Table 6. Summary of the stepwise redundancy analyses considering the 5 most common small rodent species (number of captures / small quadrate - SQ) trapped within 147 SQs. The analyses were conducted separately by using 16 vegetation parameters (a) and 6 habitat types (b) as constraining variables. The variables used are listed and described in Table 1. For each analysis we present the total inertia, the constrained inertia, the percentage of explained variation and the eigen values for the RDA axes (see text for interpretation of these parameters). The results of the permutation test of significance are presented for the first 5 environmental variables included in each model.

(a) Vegetation - RDA	Total variance		Constrained variance		Percentage of explained variation	
	13·775		4·758		34·50%	
		RDA1	RDA2	RDA3		
	Eigen values	2·616	1·667	0·433		
			Biplot scores		Permutation test	
	Constraining variables	RDA1	RDA2	RDA3	*Pseudo-F*	*P*
	Tree height	0·564	-0·250	-0·087	0·366	< 0·001
	Herb height	-0·758	-0·402	0·163	0·745	< 0·010
	Crop height	0·050	0·673	-0·198	0·302	< 0·001
	Tall berry height	0·256	-0·468	0·347	0·223	< 0·010
	Moss percentage	0·365	-0·059	-0·114	0·135	< 0·010
(b) Habitat - RDA	Total variance		Constrained variance		Percentage of explained variation	
	13·775		3·958		28·70%	
		RDA1	RDA2	RDA3		
	Eigen values	2·442	1·307	1·064		
			Biplot scores		Permutation test	
	Constraining variables	RDA1	RDA2	RDA3	*Pseudo-F*	*P*
	Abandoned meadow	0·182	0·597	0·736	0·251	< 0·001
	Meadow	-0·957	0·095	-0·075	0·968	< 0·001
	Mature forest	0·390	0·007	-0·419	0·148	< 0·010
	Young forest	0·342	0·135	-0·172	0·117	< 0·050
	Crop	0·077	-0·897	0·430	0·454	< 0·001

Table 7. Comparison between the index of species richness and the PIE Hurlbert´s indices of evenness (Hurlbert 1971) in different habitat types. The indices were calculated with the software EcoSim (Gotelli & Entsminger 2006) by standardising the sample size in each habitat type with respect to the habitat type containing the lowest number of individuals (*i.e.* crop, *n* = 86).

Habitat type	Richness			Evenness		
	Estimate	95% C.I.		Estimate	95% C.I.	
		Lower	Upper		Lower	Upper
Clearcut	6·21	4·00	8·00	0·65	0·59	0·70
Young forest	6·13	5·00	7·00	0·62	0·57	0·67
Mature forest	4·00	4·00	4·00	0·59	0·58	0·61
Crop	7·99	8·00	8·00	0·62	0·61	0.63
Meadow	4·75	4·00	5·00	0·65	0·59	0·70
Abandoned meadow	5·41	4·00	7·00	0·66	0·61	0·70

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Manuscript V

Predation risk, habitat use and distribution of alternative prey: the case of red fox, roe deer fawns, and small rodents

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Abstract

We explored direct and indirect mechanisms through which habitat can affect the probability of radio-monitored roe deer fawns *Capreolus capreolus* being killed by red foxes (*Vulpes vulpes*) in south eastern Norway. Habitat characteristics affected directly roe deer visibility and, indirectly, prey behaviour and the spatial distribution of red foxes' main prey, *i.e.* small rodents. Predation risk was mostly affected by the visibility of the mother, which could involuntarily provide cues on the fawns' locations to sit-and-wait predators; fawn visibility at bed sites was constantly low and did not affect predation risk. Predation risk increased with mother-fawn distance. However, this relationship was highly context-dependent, as mother-fawn distance varied among habitat types according to visibility, fawns' activity, age, and sex. Cultivated fields and clear-cuts represented safe hiding areas for fawns while mothers kept distant due to the high visibility. Forested habitats, in particular mature forests, represented areas where fawns could practise moving and interacted with their mothers. Notwithstanding the very limited availability of meadows, fawns used them more than any other habitat type; the does used them even more than fawns due to the availability of high-quality food and to the low visibility. However, fawns using more meadows suffered higher predation risk. Meadows were small patches particularly rich in small rodents, and we suggest that the higher red fox-roe deer encounter rate in these "hot spots" induced a higher predation risk. However, the proximity of the mother at the stage when fawns were most vulnerable to predation could limit predation risk in meadows. Even though the selection for agricultural areas, at higher spatial scales, and for meadows within the home range could seem a non-adaptive strategy, this habitat choice may reflect the does' energetic stress due to lactation.

Introduction

Due to its high variability, juvenile recruitment is the major factor shaping wild herbivores' population dynamics (Gaillard et al. 1998a; 2000). A great deal of this variability is accounted for by the mere presence or absence of predators that, where present, commonly constitute the most common cause of neonatal mortality in large ungulates (Linnell et al. 1995). Still, variation in neonatal predation rates and patterns remains considerable and poorly understood, due to the scarcity of adequate data (*i.e.* from long-term comparative studies on individually marked animals; Gaillard et al. 2000).

In this study we explored factors affecting variation in predation rates and patterns in the roe deer fawn (*Capreolus capreolus*) - red fox (*Vulpes vulpes*) system in south eastern Norway. Red foxes are opportunistic predators whose main prey are small rodents throughout their range (Lindström et al., 1994). Red foxes are also the undisputed major predator of the newborn roe deer, which represent a profitable alternative prey item suffering high predation rates (25% in our study area, Panzacchi et al., 2007b; 48% in central Norway, Aanes & Andersen 1996; up to 90% in Sweden, Jarnemo & Liberg 2005). However, roe deer fawns represent only a secondary prey item for red foxes, as in our study area their contribution to the spring-summer diet was about 10% (Panzacchi et al., 2007a). It is therefore crucial to understand factors influencing red fox population on fawns, if we are to understand the impact of the predator on roe deer population dynamics.

According to Endler (1986), a predator-prey interaction can be subdivided into the following steps: encounter, detection, identification, approach, subjugation and consumption. Hence, factors affecting each of these steps have the potential to influence predation rates and patterns.

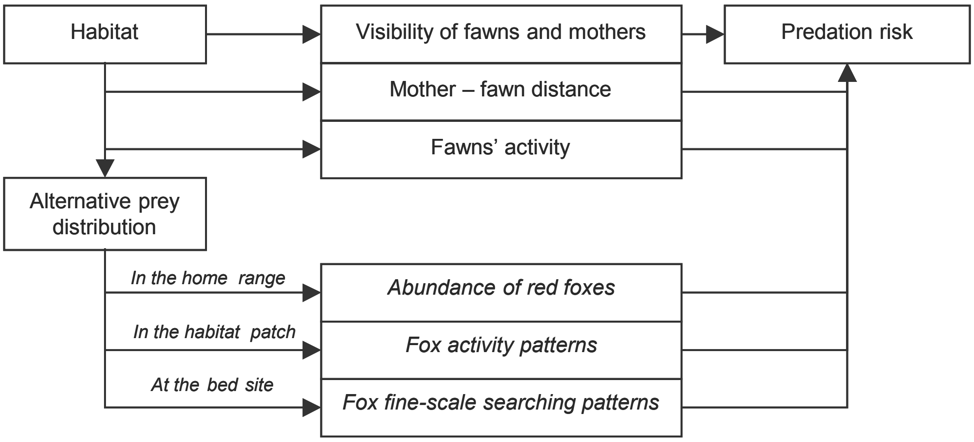
At a large spatial scale, landscape structure and composition may affect population densities of both predators and prey and, consequently, alter predator-prey encounter probabilities and predation rates. Accordingly, we have previously shown that the higher roe deer density associated with fragmented agricultural landscapes in southastern Norway induced a higher degree of feeding specialisation on the part of red foxes and higher overall neonatal predation rates compared to low-density, forest dominated areas (Panzacchi et al. 2007b, c). Furthermore, temporal variation in survival rates roe deer fawns in Sweden was positively correlated to the abundance of red foxes' main prey, *i.e.* small rodents, and negatively correlated to red fox abundance (Kjellander & Nordström 2003; Jarnemo and Liberg 2005).

At finer spatial scales, habitat structure and composition may directly and indirectly affect most of the above-mentioned steps in predator-prey interaction. Directly, habitat characteristics may alter both prey visibility (*i.e.* detection, *sensu* Endler, 1986), and the probability of a fox approaching a fawn while remaining undetected by the mother (*i.e.* approach and subjugation). Indirectly, habitat can influence prey behaviour and anti-predator behaviour, which have the potential to alter the probability of predator-prey encounter, and all others steps leading to a successful predation event. Finally, habitat structure and composition markedly affects the distribution of the red foxes' main prey species, *i.e.* small rodents (Panzacchi et al. 2007 d). The spatial distribution of red foxes' main prey, in turn, may affect the predators' searching behaviour, and the probability of encounters with roe deer. Even though these hypotheses regarding the effect of fine-scale habitat related factors in predation risk have been previously suggested, quantitative evidence of the mechanisms through which habitat affects predation risk is lacking.

In this paper we focus on fine spatial scales, *i.e.* within the spring-summer home range of roe deer family groups, and investigate direct and indirect mechanisms through which habitat can affect the probability of a fawn being killed by a fox.

Roe deer fawns adopt a hiding type of anti-predator strategy (Lent 1974), *i.e.* lie motionless, odorless, and secluded from their mothers, which keep at a certain distance in order not to attract the predators attention, and visit the offspring several times a day for care and for changing of bedding site. Hence, we expect roe deer fawns' predation risk to increase with the visibility of both mothers and fawns (*Prediction I*) and with a fawn's activity index (*Prediction II*). In addition, since direct observations have shown that the defensive intervention of roe deer mothers can be important for deterring predators (Jarnemo 2004), we expect predation risk to increase with the distance between mothers and hidden fawns (*Prediction III*). Finally, we predict that roe deer fawns hiding in areas with a higher estimated abundance of the main prey of red foxes - *i.e.* small rodents -, have a higher probability of being detected by foxes and will experience a higher predation risk (*Prediction IV*). A synthesis of the main predictions tested in this paper is presented in Fig.1.

Figure 1. Block diagram illustrating the predictions (P I, II, III, IV) explored in this paper regarding the different habitat-related mechanisms trough which habitat may affect the probability of a roe deer fawn of being killed by a red fox at different spatial scales. The suggested reasons underlying the predictions are in italic.



Methods

Study area

The study was conducted during spring-summer 2001-2004 in Østfold and Akershus counties, south-eastern Norway. The study area is situated in the hemi-boreal biogeographical zone, and it is made up of a fine mosaic of agricultural areas (24%), lakes and rivers (11%) and intensively managed even-aged forest plots (65%), for the most part coniferous (Norwegian spruce, *Picea abies*, and Scots pine, *Pinus sylvestris*) with interspersed patches of birch (*Betula spp.*) and other deciduous trees. Among roe deer predators, the study area is inhabited by a stable population of Eurasian lynx (*Lynx lynx*) and, occasionally, by wolves (*Canis lupus*); red foxes are widespread and are the major predators for roe deer fawns, being responsible for 58% of mortality causes (Panzacchi et al., 2007b). During spring the main prey items for red foxes are small rodents (*e.g. Microtus agrestis, Arvicola terrestris, Clethrionomys glareolus, Apodemus sylvaticus*), and medium-large mammals (for the most part roe deer fawns); other available prey items are represented by birds (*e.g. Tetrao tetrix, Tetrao urogallus*), vegetable items (e.g. *Vaccinium myrtillus, Rubus idaeus*) and a wide range of invertebrates (Panzacchi et al., 2007a). In accordance to previous studies showing that small rodent populations exhibit multi-annual fluctuations in abundance only above the 60° N (Hanski et al. 1991), populations inhabiting our study do not seem to be cyclic (see also Panzacchi et al., 2007d).

Roe deer fawns

Captures and monitoring

From 2001 to 2004 we captured 98 roe deer fawns, belonging to 55 different family groups, by stalking radio-collared does, or by chance when observing lactating mothers. All fawns were equipped with an expansible radio-collar and were radio-located approximately every day for the first 2 months of life, and roe deer mothers were radio-located simultaneously. While approaching the fawn, we recorded an index of activity, indicating if the fawn showed signs of activity or not. Due to collar failure, we lost contact with two of the captured fawns, which were excluded from the analyses. The intensive monitoring plan allowed us to find the carcasses of fawns soon after death, and to assess mortality causes either directly in the field or after necropsy conducted at the Norwegian Veterinary Institute, Oslo. For further details see Panzacchi et al. (2007b).

Table 1. Description of habitat and vegetation parameters recorded (i) at each roe deer fawn's bed site – *i.e.* within each 15 x 15² m quadrate surrounding each bed site; (ii) at a random point – i.e. within a 15 x 15² m quadrate 50 m distant from each bed site, in a random direction; (ii) within each Small Quadrate (SQ) - *i.e.* the 15 x 15² m area delimited by the live-traps used in the study on small rodents. Vegetation descriptors were quantified as proportion cover within each quadrate.

	Parameter	Description
(a) Habitat type	Clear-cut	
	Young forest	Young plantation and pole sized stands*
	Mature forest	Medium aged stands and mature stands*
	Crop	Cultivated fields
	Meadow	Grassy, uncultivated areas, sometimes unmanaged and slowly reverting to forest (*i.e.* with sparse trees and bushes)
(b) Vegetation descriptors	Moss	
	Herbs	Herbaceous plants
	Crop	Cultivated cereals; present/absent
	Small berries	Blueberry and cowberry
	Tall berries	Raspberry
	Bushes	Woody plants < 1.5 m
	Branches	Dead tree trunks, branches

*According to Børset et al 1985

**Not recorded in the study of small rodents*

Parameters recorded at bed-sites

In 2003 and 2004, within the 15 x 15 m² surrounding each roe deer fawns' bed-site, we recorded qualitative information regarding the main type of habitat (Table 1a), and quantitative information on vegetation cover and structure (Table 1b). In addition, an index of fawn visibility (VIS) was recorded at each bed-site by estimating the average distance from which a fawn could be visible from a red fox point of view (*i.e.* 50 cm above the ground level) in each of the four cardinal directions. A similar index was obtained for roe deer mothers (MVIS) by estimating the average distance at which a reference sample resembling their dimensions (1 m above the ground) could be detected. Whenever possible, we estimated habitat parameters and visibility indices from a certain distance in order to limit disturbance; in other cases we marked the position with a GPS and we returned to the location the following day. During 2001 and 2002, we only recorded the qualitative assessment of the habitat type within the 15 x 15 m² surrounding each roe deer fawn's bed-site. This operation was conducted either directly in the field or, afterwards, by using a combination of digitised forestry maps, 1:5000 paper forestry maps, and recent aerial photos. We controlled for habitat changes that may have occurred during the time of the study, *e.g.* clear-cutting of patches of mature forests, by comparing forestry maps and aerial photos. In total, roe deer fawns were radio-located 1498 times before their 60th day of life.

Habitat use and selection

The use of different habitat types is commonly correlated with habitat availability. Thus, the study of habitat use provides a clear indication of the time spent in each habitat patch, and is relevant in order to test for hypotheses concerning predation risk associated with time spent in different patches. On the contrary, habitat selection is relevant in order to test for hypotheses concerning the effect of behavioural choices on predation risk. We analysed roe deer habitat selection at two spatial scales: (a) selection for different habitat types at the bed sites compared to those available within the home range; (b) selection for different vegetational characteristics at the bed site compared to those available at a random point.

(a) Selection for specific habitat types

Typically in habitat selection analyses, the available area for an individual is defined as some sort of home range estimate (Manly et al. 2002). We assessed the availability of different habitat types within the 95% minimum convex polygon (MCP) calculated for each family group from capture to September the 25th. Habitat composition within the home range was calculated by using digitised forestry maps, whenever these were available, or by using a planimeter and the above-described paper forestry maps. For each home range, habitat availability was further validated by using aerial photos and in some cases also by checking directly in the field, as described above. Considering the highly fragmented landscape, the intensive forest management, the small-scale unit of management operations, and the very small scale of our sampling unit (15 x 15 m²), we assumed that the home range of each family group included at least 0.1% of each habitat type.

The probability of detecting the presence of an individual in each of the *n* different habitat types composing its home range can be estimated by using multinomial logit models, assuming that a random use would yield *n* probabilities reflecting the proportion of each habitat type available for that individual. The multinomial logit-model is the likelihood-equivalent to a Poisson log-linear model (Chen & Kuo 2001), which is easier to fit, particularly when including random effects (Chen & Kuo 2001). Random effects are highly relevant when analysing habitat selection with individual data (Gillies et al. 2006). Accordingly, we modelled the number of radiolocations in different habitat types for fawns belonging to each family group by using a generalised linear mixed model with Poisson log-linear family (Chen & Kuo 2001). Hence, all reported estimates for parameters in the habitat selection analyses are on a $\log_e$-scale. In such an approach, the number of observations inside each habitat type is expected to have a linear relationship with the proportion of area available for that specific habitat type. Furthermore, the sampling effort affects the expected number of observations in each habitat type. Since in our study the sampling effort equals the number of radio-locations, we added the proportion of different habitat types available in the home range and the number of radio-locations of the siblings belonging to the same family group as offset variables in the habitat selection models. These were first $\log_e$ -transformed to fit the log-linear model approach. Vegetation type was then added as fixed variable in the model. The estimates would then reflect the number of observation per habitat type for the average proportion of habitat types available and the average sampling effort.

In order to test for age-specific habitat selection, we split the dataset in two age classes: 0-30 days (age class I) and 31-60 days (age class II) of life. The sampling effort was split likewise in order to account for differences in number of individuals in the family during the two age classes (*e.g.* due to mortality). Then, age class was included in interaction with vegetation type. In order to avoid the influence of habitat-specific mortality on the estimation the effect of age on habitat selection, the analyses were performed at first by including all individuals and, afterwards, by including only fawns that survived throughout the study period.

Finally, we tested for differences in habitat selection between families that experienced red fox predation and those where all radio-monitored fawns survived. This was only possible for age class I because of little predation in age class II. Families were coded 1 and 0 if they had experienced red fox predation or not, respectively, and this variable was added in interaction with vegetation type in the habitat selection model. Since neonatal mortality was pronounced soon after birth, in particular due to haw-mowing machines and red fox predation (Panzacchi et al., 2007a), in the habitat selection analyses we only included families with 8 or more observations during the first 60 days, while in the analysis of habitat selection and red fox predation we included families with 5 or more observations in age-class I.

(b) Selection for vegetation cover

In order to test for the selection of bed-sites with particular characteristics of vegetation cover and indices of visibility, the same parameters recorded at bed-sites were recorded within a 15 x 15 m² quadrate centred in a random point 50 m distant, within the same habitat type chosen by the roe deer fawn. If the roe deer fawn was bedding in a very small habitat patch, we only recorded parameters at the bed sites. We compared parameters recorded at the bed-site and at the corresponding random point by using a pair-wise Wilcoxon signed rank tests.

Table 2. Set of best performing generalised linear models explaining the index of abundance of *Microtus agrestis*, *Clethrionomys glareolus* and *Apodemus sylvaticus* with vegetation descriptors (Table 1b). Models were ranked according to the Akaike Information Criterion corrected for small samples (AIC_c; Burnham and Anderson 2002), with the most parsimonious model - used afterwards for predicting the index of small rodent abundance at each roe deer fawn bed-site - on top of each list. For each model, we present the parameter estimates ($\log_e$-scale), the normalised likelihood of the model (Akaike's weights, ω_i), and the number of parameters (*k*).

Species	Model	AIC_c	ΔAIC_c	ω_i	k
C. glareolus					
	0.013 t. berry - 0.034 branch - 0.034 crop - 0.009 herb - 0.025 moss	574.7	0.000	0.521	6
	- 0.039 branch - 0.040 corp - 0.016 herb - 0.028 moss - 0.007 s. berry	576.1	1.317	0.265	6
	0.010 t. berry - 0.036 branch - 0.037 crop - 0.012 herb - 0.026 moss -0.003 s. berry	576.4	1.664	0.435	7
M. agrestis					
	0.030 branch + 0.051 bush + 0.037 crop + 0.056 herb + 0.044 t. berry	450.6	0.000	0.433	6
	0.014 bush + 0.020 herb - 0.060 moss - 0.032 s. berry	450.8	0.228	0.386	5
	0.026 branch + 0.045 bush + 0.032 crop + 0.051 herb - 0.022moss + 0.039 t. berry	452.3	1.749	0.181	7
A. sylvaticus					
	0.017 crop	300.7	0.000	0.475	2
	0.017 crop - 0.026 t. berry	301.7	0.967	0.293	3
	0.016 crop - 0.012 bush	302.2	1.433	0.232	3

Small rodents

Capture-mark-recapture study

During 2003and 2004 we performed a capture-mark recapture study on small mammals. The study design was based on Small Quadrates (SQs, Myllmäki et al. 1971), which are 15 x 15 m² trapping units composed of 12 live-traps evenly positioned along the perimeter. During the study period, 190 SQs were activated for 100 days in the six habitat types listed in Table 1a, and 1121 individual small mammals, belonging to 11 species, were trapped and individually marked. Within each SQ we recorded the same vegetation parameters as for the roe deer fawns' bed sites (Table 1). The population estimates for the three most common species (*M. agrestis*, *C. glareolus*, *A. sylvaticus*) in different habitat types were obtained using the software MARK 4.3 (White and Burnham 1999). For further details see Panzacchi et al. (2007d).

Indices of abundance

Two indices of abundance of small rodents have been calculated: SR.HAB, based on the qualitative assessment of the habitat type (Table 1a), and SR.BED, based on quantitative vegetation cover characteristics at the bed site (Table 1b). SR.HAB reflects the number of small rodents estimated by the capture-mark-recapture study in each habitat type, per area unit (Table 5). Hence, this index is not bed-site specific, but indicates the number of small rodents at a wider spatial scale, *i.e.* the habitat patch a fawn was bedding in. On the contrary, SR.BED was calculated specifically for each 15 x 15 m² surrounding each roe deer fawn's bed site by predicting therein the number of small rodents inside it. First, for each of the three above mentioned most common species we modelled the number of individuals captured during 10 days with the vegetation cover characteristics recorded within each SQ (Table 2). These analyses were performed by using generalised linear models and assuming a negative binomial distribution, which is commonly used to describe the distribution of count data in which the variance is greater than the mean (*i.e.* over-dispersed Poisson distribution; Crawley, 2002). After, we used the parameter estimates from the most parsimonious model to predict the number of small rodents within the 15 x 15 m² surrounding each fawn's bed-site. Both indices were corrected for red fox preferences for different species of small rodents, based on the results of our previous study on red fox diet (Panzacchi et al., 2007a). The correction factor was obtained by multiplying the number of *M. agrestis* (preferred prey) by 1.00, *C. glareolus* by 0.077, and *A. sylvaticus* by 0.038, according to their frequency of occurrence relative to the field voles in the diet.

Table 3. Roe deer fawn's habitat selection during spring-summer 2001-2004 in southeastern Norway. Estimates of the difference in overall habitat selection for roe deer fawns during summer. Above the diagonal is given the estimate of difference (SE), below the corresponding z-values and p-values. All estimates are on a loge -scale.

	Clear-cut	Crop	Meadow	Mature forest	Young forest
Clear-cut		-0. 760 (0.107)	1.301 (0.105)	-0.255 (0.102)	-0.477 (0.107)
Crop	z = -7.12, p < 0.001		2.058 (0.080)	0.503 (0.079)	0.280 (0.085)
Meadow	z = 12.36, p < 0.001	z = 25.83, p < 0.001		-1.554 (0.077)	-1.777 (0.082)
Mature forest	z = -2.50, p = 0.012	z = 6.35, p < 0.001	z = -20.13, p < 0.001		-0.223 (0.081)
Young forest	z = -4.44, p < 0.001	z = 3.31, p = 0.001	z = -21.74, p < 0.001	z = -2.77, p = 0.006	

Factors affecting predation risk

We investigated the relationship between habitat types and the index of roe deer visibility, mother-fawn distance, and fawn activity. Then, we explored the influence of rodent abundance, and these habitat-related parameters on roe deer fawns' predation risk using univariate generalised linear models, considering the fate of each fawn (killed *vs.* alive) at each bed-site as a dependent variable, with binomial distribution. The analyses were repeated using general linear mixed models in order to correct for the interdependence at the roe deer family scale (random factor = "family"). The analyses were carried out both considering the first month of life, and by comparing the last 5 locations before death - for fawns that were killed by fox -, with the five locations before the average age at which predation occurred in our study area (22 ± 13 days, n = 21) - for fawns that survived. In this last case, considering the non-independence among siblings in predation risk (Panzacchi et al., 2007c), for each family that suffered from predation we only considered data referring to the first fawn that was killed. Finally, we investigated the relative effect of the above-mentioned habitat related parameters on predation risk by using multivariate logistic regression models. The full model contained roe deer fawns' predation risk (killed *vs.* not killed) as a dependent variable, and visibility, mother-fawn distance, activity, and abundance of small rodents. Model selection was based on AIC_c, according to Burnham and Anderson (2002). All analyses were done in R version 2.4.0 for windows (R Development Core Team 2006), where general linear mixed models were fitted using the lmer-function in the lme4 package (Bates & Sarkar 2006). The evaluation of the significance of the estimated parameters was done by Fisher z-statistics. If not otherwise stated, mean values are followed by standard deviation.

Results

Small rodents and vegetation

The three most parsimonious models explaining the abundance of the three most important small rodent species are presented in Table 2. The abundance of *C. glareolus* was positively related to the proportion of raspberries ($p = 0.045$) and negatively related to moss ($p = 0.014$), herbaceous plants ($p = 0.003$), crop and branches ($p < 0.001$). The abundance of *M. agrestis* was positively related to the proportion of herbaceous plants, raspberries, bushes, branches and crop ($p < 0.001$). Finally, *A. sylvaticus* was positively related only to the presence of crop ($p < 0.001$).

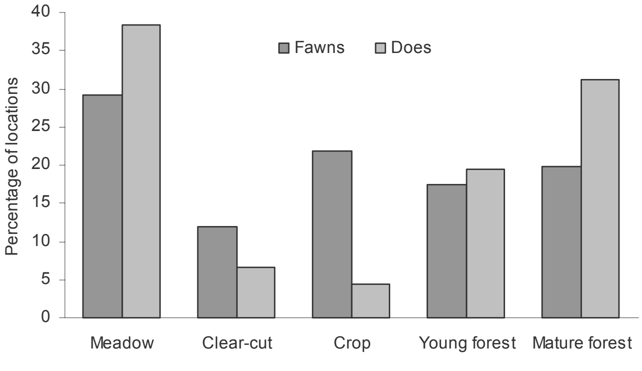


Figure 2. Habitat used by roe deer fawns and mothers in south eastern Norway, expressed as percentage of radiolocations in different habitat types during the fawns' first month of life.

Roe deer habitat use

Within all roe deer fawn home ranges, the most common habitat type available were crops (38%), followed by mature forests (27%), young forests (24%), clear-cuts (6%) and meadows (5%). During the first month of life, fawns used meadows more than any other habitat type, while clear-cuts were used less than expected under the null hypothesis of no differences in habitat use ($\chi^2_4 = 59.271$, $p < 0.001$, Fig. 2). However, fawns used more clear-cuts ($z_{1092, 1088} = 5.785$, $p < 0.001$) and crops ($z = 2.892$, $p = 0.004$), and less mature forests ($z = -3.866$, $p < 0.001$), meadows ($z = -3.292$, $p = 0.001$) and young forests ($z = -2.456$, $p = 0.014$) than their mothers (Fig. 2). During the same period, roe deer mothers used more meadows and less cultivated fields than expected ($\chi^2_4 = 43.980$, $p < 0.001$). Habitat use changed from the first to the second month of life. During the second month, mature forest was the most frequently used habitat type, while clear-cuts were the least frequently used ($\chi^2_4 = 96.167$, $p < 0.001$). From the first to the second month roe deer mothers increased the use of crop ($z_{545,541} = 2.176$, $p = 0.030$) and, during the second month, they used less clear-cuts and more meadow and mature forest than expected ($\chi^2_4 = 25.100$, $p < 0.001$).

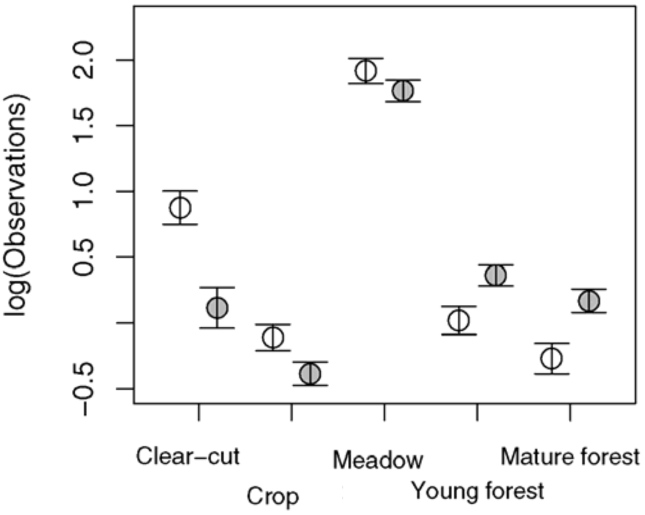


Figure 3. Difference in roe deer habitat selection between fawns belonging to age class I (0 - 30 days, colour only) and age class II (30 - 60 days, black circle). Bars indicate standard deviation of the estimate. The estimated number of $\log_e$ (observations) per habitat class refers to an average proportion of habitat availability and average sampling effort for all families.

Roe deer fawns' habitat selection

Selection for habitat types

The overall preference differed among habitat types. Habitat selection was highest for meadow, followed by clear-cut, mature forest, young forest, and finally crop. The difference in selection among all habitat types was significant (Table 3).

Age-specific selection for habitat types

Habitat selection changed from the first to the second month of life. The pattern was consistent if we included all individuals, or only those that survived. We only present the latter here. During the first month of life, habitat selection was greatest for meadow, followed by clear-cut, mature forest, young forest and crop (Fig. 3). The utilisation of clear-cut (estimate = -0.796, $z = -3.99$, $p < 0.001$) and crop (estimate = -0.277, $z = -2.27$, $p = 0.023$) decreased significantly from the first to the second month of life (Fig. 3), while it increased for mature forest (estimate = 0.341, $z = 2.86$, $p < 0.004$) and young forest (estimate = 0.441, $z = 3.27$, $p < 0.001$). Accordingly, the ranking of the habitat types changed to (in decreasing order of preference) meadow, mature forest, young forest, clear-cut and crop. However, the difference in selection between clear-cut and mature forest (estimate of difference = 0.243, $z = 1.49$, $p = 0.135$), clear-cut and young forest (estimate = 0.050, $z = 0.30$, $p = 0.767$) and young forest and mature forest (estimate = 0.192, $z = 1.83$, $p = 0.068$) were not significant for the second month of life. All other differences were significant within the age classes.

Figure 4. Habitat used by fawns vs. predation risk: comparison between the habitat types recorded at the last five locations before a roe deer fawn was killed by red fox (dark bars), and the habitat type recorded at the five locations preceding the average age a fawn was killed by fox (22 ± 13 days, $n = 21$) - for fawns that survived (light bars). Given the non-independence among siblings in predation risk (Panzacchi et al., 2007c), for each family group we only considered the first fawn that was killed by red fox.

Selection for specific vegetation characteristics

The comparison between parameters recorded at bed sites and at the random sites revealed a strong selection for bed sites with lower indices of visibility for both the fawns and their mothers (Table 4a). Following the seasonal development of the vegetation (Table 4b), fawn visibility decreased from the first to the second month of life. During their first month roe deer fawns selected for areas characterised by a higher average height of herbaceous vegetation, a higher proportion of bushes, and a lower proportion of moss compared to random sites (Table 3b). During their second month fawns selected bed sites containing still a higher average height of herbaceous vegetation, a higher proportion of berry-bushes, and a lower proportion of branches. Contrary to our hypothesis, the estimated number of small rodents at bed sites was not lower compared to random sites (Table 3c).

Table 4. Pair-wise comparison between parameters recorded at each roe deer fawn's bed site (mean, St.d.) and at the corresponding control sites (mean, St.d, n) during 2003-4. We compared: (a) indices of visibility of fawns (VIS) and mothers (MVIS, in m); (b) proportion vegetation cover (Prop.) and height (Height, in cm); (c) indices of abundance of small rodents (SR.BED). Results are presented separately for fawns belonging to age 0-30 days, and 31-60 days. We used Match-pair Wilcoxon rank tests to compare beds and random sites, and two-samples Wilcoxon test for comparisons between different age classes. One-tailed tests in (a) and (c), two tailed in (b); symbols indicate significant differences (** p <0.001; * p < 0.05).

			Age class I			Age class II			Age class I *vs*. II	
			Bed-site		Random	Bed-site		Random	Bed-site	Random
(a)	Visibility	VIS	0.8 (2.5)	<**	3.8 (11.5, 264)	0.2 (0.8)	<**	1.2 (3.0, 116)	>**	>**
		MVIS	31.8 (30.9)	<**	40.9 (38.6, 206)	31.7 (32.5)	<**	50.6 (54.0, 65)		
(b)	Grass	Height	62.5 (36.1)	>**	51.2 (36.7 166)	85.9 (46.6)	>*	80.9 (52.3, 100)	<**	<**
		Prop.	34.5 (38.4)		36.4 (40.8, 350)	48.7 (41.8)		46.5 (40.9, 167)	<**	<**
	Moss	Height	6.5 (3.5)		7.1 (4.3, 42)	12.5 (14.6)		5.5 (1.6, 10)		
		Prop.	5.1 (15.1)	<**	7.0 (16.9, 350)	4.1 (15.9)		2.3 (6.4, 167)	>*	>*
	Small berry	Height	26.4 (14.4)		24.7 (12.1, 23)	16.3 (2.3)		17.5 (4.6, 8)	>*	
		Prop.	5.8 (18.4)		7.0 (18.8, 350)	2.0 (10.7)		2.8 (12.0, 167)	>*	>**
	Tall berry	Height	97.8 (28.4)		97.3 (28.5, 28)	95.0 (71.3)		101.7 (71.3, 12)		
		Prop.	8.1 (22.6)		7.1 (22.4, 350)	6.7 (17.9)	>*	4.0 (14.4, 167)		
	Bush	Height	94.3 (33.5)		93.9 (36.8, 40)	123.9 (55.5)		110.0 (59.2, 26)	<*	
		Prop.	12.3 (24.0)	>**	7.4 (19.4, 350)	9.5 (17.9)		8.1 (18.3,167)		
	Crop	Height	88.7 (39.1)		86.2 (39.1, 70)	97.8 (31.3)		97.8 (35.8, 38)	<**	<**
		Prop.	22.3 (41.7)	<*	23.5 (42.4, 350)	22.6 (42.0)		25.6 (43.8, 168)		
	Branches	Height	47.7 (15.2)		42.2 (27.1, 35)	55.9 (22.0)		57.6 (27.6, 17)		<**
		Prop.	10.4 (26.1)		10.7 (25.5, 350)	4.8 (13.6)	<**	8.3 (19.5, 167)	>**	
(c)	SR.BED		1.5 (1.2)		1.4 (1.2, 350)	1.9 (1.2)		1.7 (1.3, 168)	<**	<**

Visibility, activity and mother-fawn distance

Variations among habitat types in the distance between mothers and fawns, in the indices of visibility, and in the index of fawns' activity are illustrated in table 5 b, c, d. During the first month of life, roe deer fawns were on average 94 ± 134 m (n = 327) from their mothers, and this distance was correlated with the index of visibility of the doe at the bed site (Spearman, $r = 0.246$, $p < 0.001$). The distance between mothers and fawns decreased with age (31-60 days: 87 ± 143 m, n = 202; $r = -0.099$, $p = 0.013$), and the change was more marked for female fawns ($r = -0.172$, $p = 0.008$) than for males ($r = -0.036$, $p = 0.541$). Fawn activity was negatively associated with mother-fawn distance (0-30 days: $z_{283,282} = -3.656$, $p < 0.001$; 0-60 days: $z_{457,\,456} = -2.335$, $p < 0.020$), indicating that fawns were active for the most part when associated with the mother. In fact, the average distance between mothers and fawns was 22 ± 49 m (n = 35) when fawns were active, while it increased up to 103 ± 144 m (n = 386) when fawns were not active. The average mother-fawn distance in different habitat types varied with the fawns' activity: when fawns were active, the distance was null in mature forests (1 ± 0, n = 17), followed by young forests (34 ± 51, n = 7) and meadows (47 ± 73, n = 9). On the contrary, when fawns were not active the distance decreased in the order: mature forest (141 ± 197, n = 51), clear-cut (136 ± 150, n = 59), crop (134 ± 142, 86), young forest (96 ± 134, n = 61) and meadow (79 ± 47, n = 129). The percentage of times a fawn was active increased from the first (8%, n = 421) to the second month of life (24%, n = 285; $\chi^2_1 = 31.572$, df = 1, $p < 0.001$), and was not affected by sex ($\chi^2_1 = 0.011$, $p = 0.916$).

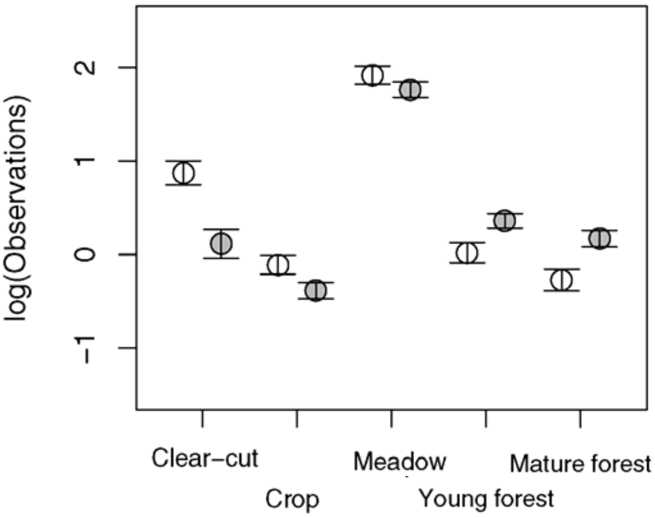


Figure 5. Habitat selection *vs*. predation risk: difference in habitat selection between families where all siblings survived (grey filled circles) and families where at least one fawn was killed by red fox (black circle) during the first month of life. Bars indicate standard deviation of the estimate. The estimated number of $\log_e$ (observations) per habitat class refers to an average proportion of habitat availability and average sampling effort for all families.

Habitat-specific predation risk

Habitat use vs. predation risk

We tested for differences in habitat use between fawns that were killed by foxes and survivors (a) during the first 30 days of life and (b) during the last 5 locations before death. In all cases, the main results were consistent: fawns killed by fox used less clear-cuts (a: GLM,: $z_{672,668}$ = -6.003, p < 0.001; b: $z_{275,271}$ = -3.714, p < 0.001) and more meadows (a: $z_{672,668}$ = 1.697, p = 0.089; b: $z_{275,271}$ = 2.478, p = 0.013) compared to survivors (Fig. 4). In addition, just before death (b), fawns killed by fox used more young forests compared to survivors ($z_{275,271}$ = 2.259, p = 0.024). When repeating the analyses with "family group" identity as a random effect in a generalised linear mixed model approach, none of the results were significant (p > 0.3). The habitat used by roe deer mothers affected the risk of predation of their fawns. In particular, the probability of fawns being killed by foxes was higher if the mother used less clear-cuts (a: $z_{305, 301}$ = -3.105, p = 0.002; b: $z_{275,271}$ = -3.714, p < 0.001). Predation risk was also higher if the mother used more crop during the first month of life (a: $z_{305, 301}$ = 2.755, p = 0.006) and, more meadows and young forests, just before the death of the fawn (b: $z_{275,271}$ = 2.487, p = 0.013; z = 2.259, p = 0.024, respectively).

Habitat selection vs. predation risk

There were only 8 families that experienced red fox predation and had 5 or more observations of fawn bed sites during the first month of life, and these families had an average of 24 (range: 7 - 48) observations. Red fox predation was not observed in 28 families, with an average number of observations in the first month of 17.75 (range: 5 - 53). The low number of families experiencing fox predation suggests that the results regarding analysis of habitat selection and red fox predation should be interpreted with caution. There were no significant differences between families where all fawns survived, and families that experienced predation by red fox during the first month in the preference for mature forest (estimate of difference: -0.166, se = 0.211, z = -0.79, p = 0.431) and young forest (estimate of difference: 0.310, se = 0.210, z = 1.48, p = 0.140; Fig. 5). However, the selection for clear-cut (estimate of difference: -0.693, se = 0.307, z = -2.26, p = 0.024), crop (estimate of difference: -0.666, se = 0.250, z = -2.66, p = 0.008) and meadow (estimate of difference: -0.495, se = 0.160, z = -3.10, p = 0.002) was significantly lower among families that experienced red fox predation compared to those that did not. However, this did not influence the ranking of the habitats noticeably.

Abundance of small rodents *vs.* predation risk

Considering only family groups with more than 10 locations - thus, excluding fawns that were killed at a very young age by foxes -, our results showed a tendency toward a higher estimated abundance of small rodents in the home ranges of family groups that suffered from red fox predation (n = 8) compared to survivors (n = 27; SR.HAB: killed, 27.801 ± 13.136, alive, 21.686 ± 6.107, GLM, $z_{34,33}$ = 1.671, p = 0.095). The likelihood of a fawn being killed by a red fox increased with the abundance of small rodents during the last days before predation occurred - or, for fawns that survived, before the average age at death (Table 5 a). This pattern was significant both at the bed site-scale and at the habitat-patch scale. However, this relationship vanished when considering the whole first month of life, or when performing the models with family groups or individual fawns nested in family group as random effect (all p-values of the estimates > 0.30).

Table 5. Differences among habitat types in the: (a) indices of abundance of small rodents at bed site and at the habitat patch; (b) distance between mothers and fawns; (c) index of roe deer fawns' activity; (d), indices of visibility at bed site and at random points. Results are presented for fawns (F) and for mothers (M), and for different age classes: age class I (0-30 days), and before death (Bef. d., *i.e.* considering only the last five locations before death for fawns killed by fox or, for survivors, before the average age at fox predation, 22 ± 13 days, n = 21). Activity is expressed as percentage of times the fawn was active (n); in all other cases, variables are expressed as average values (St. dev, n). On the right, results of logistic regression models investigating roe deer fawns' predation risk (dependent variable: killed *vs*. alive) in relation to the variables indicated on the corresponding row; p-values < 0.05 in bold characters; ° p < 0.1.

	Parameter	Age class	Unit	Habitat type					Predation risk		
				Meadow	Clear-cut	Crop	Young forest	Mature forest	z	df	p
(a)	SR.BED (at bed site, n)	I	F	2.7 (0.8, 201)	1.4 (1.0, 82)	0.5 (0.1, 137)	1.6 (1.2, 117)	0.8 (1.1, 136)	-0.770	412	0.441
		Bef. d.	F	2.9 (0.8, 68)	1.3 (0.9, 33)	0.5 (0.0, 65)	1.3 (1.2, 53)	1.2 (1.1, 62)	2.133	140	**0.033**
	SR.HAB (at habitat patch, n*)	I	F	103.4	41.0	20.0	16.3	5.9	0.170	672	0.865
		Bef. d.	F	103.4	41.0	20.0	16.3	5.9	2.123	275	**0.001**
(b)	DISTANCE (m)	I	MF	72 (124, 118)	127 (139, 47)	134 (141, 66)	77 (116, 55)	75 (152, 41)	2.215	326	**0.027**
		Bef. d	MF	77 (177, 29)	198 (194, 16)	132 (113, 32)	77 (61, 23)	34 (75, 16)	1.854	115	0.064 °
(c)	ACTIVITY (% active)	I	F	7% (138)	0% (59)	1% (87)	10% (68)	26% (69)	-1.973	420	**0.048**
		Bef. d.	F	10% (40)	0% (17)	0% (36)	10% (31)	34% (35)	-1.676	158	0.094 °
(d)	VIS (at bed site, m)	I	F	0.4 (0.6, 122)	1.4 (4.0, 66)	0.1 (0.1, 69)	1.2 (2.4, 54)	2.4 (2.9, 33)	0.484	343	0.628
		I	M	22.8 (26.4, 105)	38.1 (26.5, 57)	61.3 (47.2, 49)	9.0 (14.2, 47)	18.8 (12.1, 23)	2.803	280	**0.005**
		Bef. d	F	0.5 (0.9, 32)	0.4 (0.5, 24)	0.2 (0.2, 25)	1.3 (3.0, 23)	0.9 (1.2, 11)	0.484	114	0.628
		Bef. d	M	24.3 (28.5, 29)	28.2 (20.2, 21)	60.4 (37.8, 16)	9.1 (11.5, 20)	15.0 (5.3, 7)	2.128	92	**0.033**
	RVIS (at random point, m)	I	F	5.5 (15.4, 87)	1.6 (3.5, 47)	4.0 (16.1, 49)	2.8 (2.7, 40)	5.9 (3.0, 26)	1.555	215	0.120
		I	M	29.9 (26.9, 70)	58.5 (28.0, 39)	76.2 (48.6, 39)	8.0 (5.7, 35)	17.7 (7.1, 20)	3.646	176	**> 0.001**
		Bef. d	F	7.5 (22.7, 16)	1.4 (1.4, 16)	10.2 (25.1, 19)	3.3 (3.0, 19)	5.0 (3.6, 14)	1.283	86	0.200
		Bef. d	M	37.0 (35.2, 14)	58.7 (34.9, 13)	76.0 (39.7, 16)	9.5 (6.4, 16)	15.7 (4.8, 11)	2.422	69	**0.015**

* The standard error of the estimated population size (see Panzacchi et al., 2007d) is not shown here because the values have been corrected for species-specific fox preferences

Visibility, activity and mother-fawn distance *vs.* predation risk

As indicated by the results of the univariate models presented in Table 5, predation risk increased with the distance between mother and fawn (Table 5 b), and with the visibility of roe deer mothers (but not of fawns) at bed sites and at the random point, both when considering the whole first month of life or only the last locations before a fawn was killed by fox (Table 5 d). Unexpectedly, predation risk markedly decreased with fawn's activity (Table 5 c). Actually, a fawn that would be killed by foxes had been monitored while active in only one case out of 421. When repeating all these univariate analyses with "family" as a random effect in a generalised mixed model approach, none of the discussed variables had a significant effect on predation risk (all p values of the estimates > 0.2).

Table 6. Set of best performing logistic regression models explaining roe deer fawns' risk of predation (dependent variable: killed *vs*. alive) during the first month of life. The full model included: the indices of visibility recorded for fawns and mothers at the bed site (VIS, MVIS) and at the random point (RVIS, RMVIS), the indices of abundance of small rodents at the bed site (SR.BED) and at the habitat type (SR.HAB), the distance between mother and fawn (DISTANCE), and fawns' activity (ACTIVITY). Models were ranked according to the Akaike Information Criterion corrected for small samples (AICc), with the most parsimonious model on top of each list. For each model, we indicate the Akaike's weights (ω_i), the number of parameters (k), and the significance of the parameter estimate (*p < 0.05; ** p < 0.01).

Model	AIC$_c$	ΔAIC$_c$	ω_i	k
RMVIS**	130.316	0.000	0.391	2
RMVIS** + SR.BED	130.693	0.377	0.323	3
RMVIS** + SR.BED + ACTIVITY	130.936	0.620	0.286	4

As distance between mothers and fawns varied among habitat types, we also tested for the effect of the interaction between habitat type and mother-fawn distance on predation risk. The result showed that predation risk during the first month was significantly higher at higher mother-fawn distances when fawns were hiding in mature forests (GLM, $z_{326, 321} = 2.013$, $p = 0.044$) and also, even though not significantly, in meadows ($z_{326, 321} = 1.455$, $p = 0.145$). When repeating the analyses only considering the last locations before death, a higher mother-fawn distance when the fawn was hiding in meadows lead to a higher risk of predation ($z_{115, 110} = 2.127$, $p = 0.033$).

In Table 6 (a) we present the most parsimonious logistic regression models explaining roe deer fawns' predation risk in relation to all the variables described in Table 5. Among all variables, the index of visibility of roe deer mothers measured at a random point within the same habitat patch where the fawn was hiding had the highest effect on predation risk during the first month of life $z_{112, 111} = 3.073$, $p = 0.002$). However, according to Burnham and Anderson (2002) models with Δ AICc < 2 should not be discarded and, thus, also the second and third models starting from the top the list (Table 6) did not perform worse compared to the first model. When repeating the same analyses considering the family group identity as random effect, the null model was the best model for all age classes. We did not repeat the analyses considering the overall two first months of life, due to confounding effect of age on most of the parameters investigated, nor considering only the last locations before death due to the reduced sample size.

Discussion

Firstly, this study reveals the complexity of factors affecting predator-prey interactions on fine spatial scales. We succeeded in demonstrating a few of the direct and indirect mechanisms through which habitat can affect the probability of a fawn being killed by red foxes: through altered visibility, mother-fawn distance, fawns' activity and distribution of the main prey of red foxes. However, since these factors interacted and contributed to predation risk in a context-dependent way, we conducted the analyses and discuss the results both horizontally, *i.e.* according to different habitat types, and vertically, *i.e.* irrespective of habitat types, according to visibility, mother-fawn distance, fawns' activity and distribution of alternative prey.

The results of the latter approach indicated that *Prediction I, i.e.* that predation risk increased with visibility, was only partly supported, as it increased with all indices of a does' visibility at all the considered age classes but did not vary with any of the indices of visibility of their fawns. However, this result was not surprising considering that fawns strongly selected for bed sites with extremely low visibility, averaging 80 cm during the first month of life and 20 cm during the second, with little variability (see also Linnell et al., 2004). Hence, hiding in low-visibility bed-sites seems to be a very efficient anti-predator strategy adopted by all roe deer fawns, and their mothers' ability to select low-visibility habitat patches is more important in affecting predation risk. *Prediction III* was also supported, as predation risk increased with the distance between mothers and fawns at all the considered age classes. However, mother-fawn distance varied in different habitat types with respect to the mothers' visibility, to fawns' activity and, also, to the interaction age-sex and activity-habitat type. Thus, its effect on predation risk was highly context-dependent and, in this case too, the mothers' ability to modulate the distance to her fawn plays a fundamental role for a fawns' survival (Fitzgibbon 1993). Mothers seems to face a trade-off between being close enough to their fawn in order to defend it, and being distant enough so as to not provide cues to a predator regarding the location of their fawns. *Prediction II, i.e.* that predation risk increases with fawns' activity, was not supported. On the contrary, a fawn that would later be killed by fox was monitored while active in only one case out of 421 during the first month of life. Activity increased from 8% to 24% from the first to the second month of life, but considering that fawns were killed on average at age 22 days this result does not seem to be related to the age-specific increase in activity. Activity occurred for the most part when fawns were associated with the mother, thus supporting previous findings indicating that the behaviour of the does play a relevant role in deterring the predator (see also Jarnemo 2004).

According to *Prediction IV*, predation risk increased for fawns that used bed-sites with a higher estimated abundance of small rodents during the last days before death or before the average age at fox predation. The result was supported both at the habitat-patch scale and at the bed site scale, but not when considering the overall first month of life. Thus, our results support the hypothesis that the distribution of main prey (rodents) affects predation risk of the alternative prey (fawns), but only at the age when fawns are most vulnerable.

However, the final model indicating the relative effect of all the interacting factors discussed above clearly showed that the index of visibility of the mother in the habitat patch where the fawns was hiding was the most relevant factor explaining predation risk, during the overall first month of life. Unfortunately, we could not further explore the topic by performing model selection considering only the last locations before death due to a small sample size. Hence, the doe commonly succeeded in select bed sites characterised by optimal cover for their fawns. Most important, they have to select suitable habitat patches for the bed site simultaneously allowing them to feed, move, and rest in the surroundings of their fawns while being little visible.

The type of habitat offering the lowest vegetation cover for roe deer does was crop (Fig. 6 d). Accordingly, mothers used crops significantly less often compared to their fawns and, when they did, the likelihood of their fawns being killed by foxes increased significantly. Hence, when fawns were hiding in fields, mothers maintained a longer distance (Fig. 6 e). On the contrary, crops represented a safe place for fawns, which used them often due to the extremely low visibility index (Fig. 6 a). The probability of a fawn being killed by fox was higher for those that selected crops less during the first month of life (Fig. 5). Fawns bedding in crops were never active and (Fig. 6 e), as they grew up, the selection for fields significantly decreased (Fig. 3), further suggesting that this habitat type was used specifically in order to limit predation risk during the most vulnerable period. The fact that the overall selection for fields was low is related to the fact that only field margins were used (average distance to edge from bed sites: 23 ± 16, n = 112; from random sites: 49 ± 34, n = 85), as the does could not expose themselves too much and lead the fawn to hide in the middle of a field. In addition, the low selection for fields at this spatial scale was related to the high availability in their home ranges, which reflect a strong selection for agricultural areas at a higher spatial scale (Panzacchi et al. 2007c).

Clear-cuts represented an even safer habitat type than cultivated fields. Fawns that survived used them and selected them more compared to those that were killed by fox, and used them more than their mothers (Figs. 2, 3). Indeed, most clear-cuts were open areas with tree stumps and branches, without any forage resources for the mother. Crouched fawns in hiding position, *i.e.* with the head down, are not more than about fifteen centimetres tall, and woody debris and broken branches create lots of optimal hiding "holes" were fawns could be well hidden. Hence, in this case too, mothers kept relatively far from the hiding fawns (Fig. 6 e). Notice that both crops and clear-cuts are commonly very homogeneous habitat types sustaining a low abundance of small rodents and not offering any other alternative prey item for red foxes. Hence, it is not efficient to search randomly for fawns in these habitat types, and we can speculate that foxes can locate them only through cues involuntarily provided by roe deer does. Observations by Jarnemo (2004) in cultivated fields support this hypothesis.

Young forests seemed to be a rather neutral habitat type, not selected for and not particularly risky when considering the overall first month of life. However, when considering only the age when fawns were more vulnerable to fox predation, predation risk was higher in young forests. Fawns were sometimes active while the mother was not present, even though the visibility was high at random points and at the bed sites (Fig. 6 h, c, a). The selection for young forest, as for old forest, increased from the first to the second month of life (Fig. 3), indicating that forested habitats were used at the end of the hiding phase, when fawns started following their mothers. In particular, mature forests were the optimal place where mothers and fawns could be active together. The average distance between mothers and fawns was zero when fawns were active, and highest when they were hiding, probably in relation to the highest visibility values recorded for fawns both at random points and at the bed site. However, a high mother-fawn distance was particularly risky when fawns were bedding in mature forests, suggesting that this habitat type was not the safest for hiding.

Meadows were a key habitat type. We defined "meadows" as abandoned old fields slowly reverting into forests or semi-natural grasslands characterised by thick and high herbaceous vegetation for most of the spring and summer. The availability in the study area was minimal (5%) but, still, fawns showed a remarkably high selection for this habitat type (see also Linnell et al., 2004; Fig. 3). However, mothers spent significantly more time in meadows than fawns, probably in relation to the well-known high availability and diversity of nutritious plant species, budding at different times during spring and summer

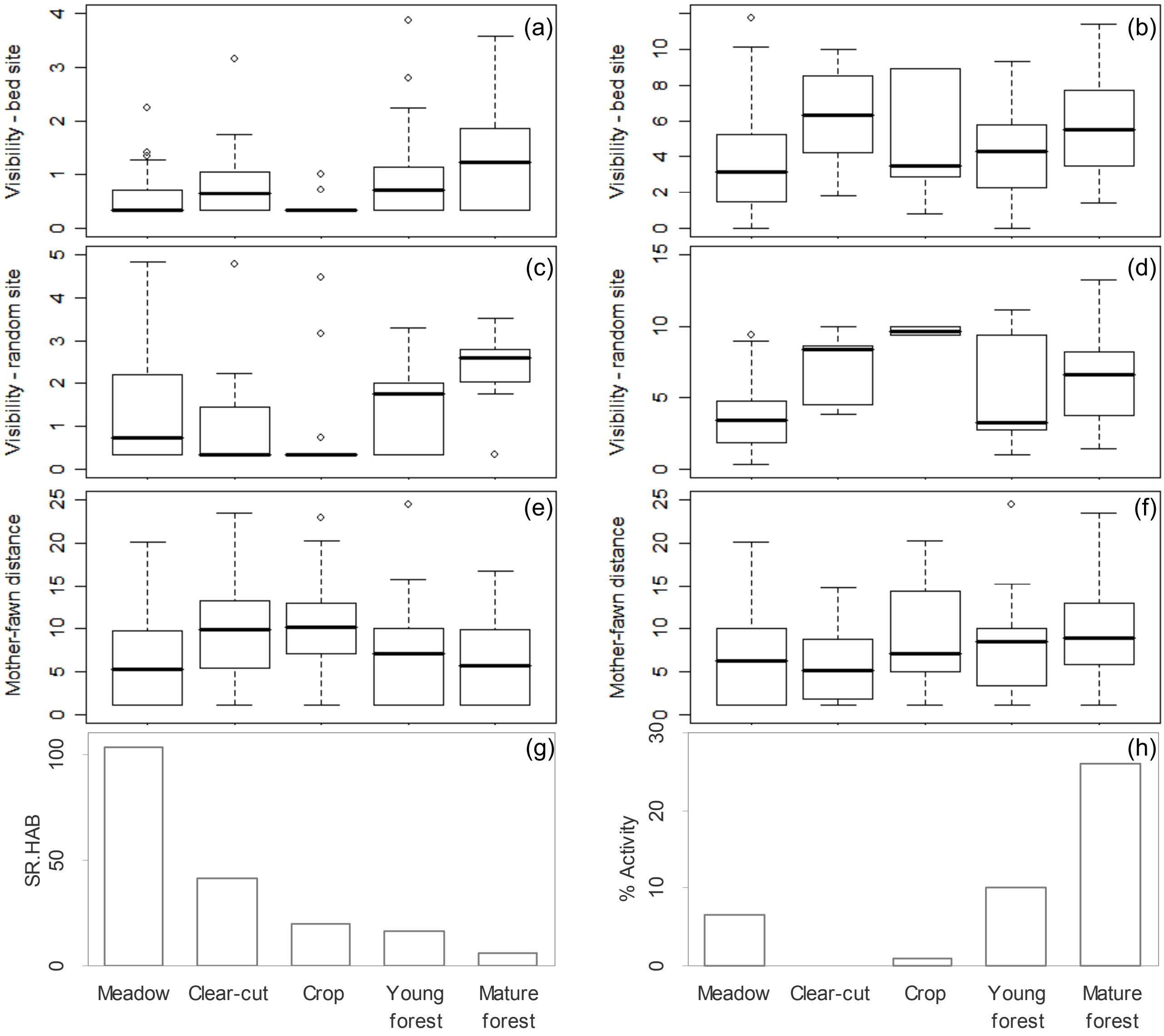
(Rosef and Bele 2005; Fig. 2). When the does were feeding in meadows, fawns were hiding close by and both their indices of visibility were on average very low. However, fawns using more meadows had a significantly higher probability of being killed by a fox both when considering the overall first month of life and, even more markedly, when considering only the most vulnerable period (Fig. 4). Why were meadows so risky? The most striking feature of meadows was their low availability and their remarkably higher abundance of small rodents at all spatial scales, compared to other habitat types (Fig. 6 g). We previously suggested (Panzacchi et al., 2007d) that meadows represent a surplus-habitat for several species of small rodents, in particular for *M. agrestis* in the more herbaceous patches, and *C. glareolus* in those more structurally complex, *i.e.* with bushes, berries or scattered trees. Considering that *M. agrestis* is by far the most preferred prey species for red foxes (Panzacchi et al., 2007a), it is reasonable to expect a higher predator activity in this habitat type. Accordingly, fawns using more meadows, *i.e.,* those being exposed for longer time in potential “red fox hot spots”, had a higher probability of being killed by a fox. In particular, the use of bed sites with a higher estimated abundance of small rodents lead to a higher predation risk at the most vulnerable stage for roe deer fawns. At this stage, predation risk increased with mother-fawn distance in this habitat type. Hence, we suggest that meadows are “hot spots” for red foxes, and represent a dangerous habitat particularly if the mothers leave their fawns alone at the stage when these are most vulnerable.

When considering the family group as random effect in our analyses, none of the results discussed were significant. This indirectly supports previous findings (Panzacchi et al., 2007c) showing the existence of family effects, *i.e.* non-independence among siblings, in predation risk. After a fox killed a fawn, the probability of a sibling being killed increased from 20% up to 42%, and predation occurred on average after 5 days. Hence, our results support the suggestion that red foxes adopt a win-stay-strategy (Olton et al. 1981), and are able to track back the family group and kill the remaining fawns, irrespectively of the habitat used or of the behaviour.

In conclusion, this study showed that fine-scale habitat characteristics affect predation risk mostly by determining mothers’ visibility (*i.e.*, prey “detection”, *sensu* Endler, 1986) and influencing predator-prey encounter probabilities. While crops and clear-cuts represented safe hiding areas for fawns, forested habitats represented areas where fawns can practise moving and interact with their mothers. Meadows were small patches rich in small rodents, which attracted red foxes and represented a risky habitat type for roe deer fawns. However, all of our results strongly support the hypothesis that the ability of roe deer does in limiting their visibility, modulating the distance to her fawn, and choosing the most appropriate habitat patches and the most safe bed sites for her fawns avoiding being predictable is crucial for their survival.

Even though the pronounced selection for agricultural areas, at the home range scale, and for meadows, at the habitat patch-scale, could seem to be a non-adaptive strategy, this habitat choice reflect the does’ particularly high energetic stress due to pregnancy and lactation (Andersen et al., 2000; Clutton-Brock, et al. 1989). However, this high-risk high-gain habitat choice is likely to have direct repercussions on the fawn’s future survival probabilities. Recently several authors have demonstrated that access to high-quality resources is closely related to the body mass of fawns in winter and consequently to winter survival, age at maturity (Gaillard et al., 1993), adult body weight (Pettorelli et al., 2002, 2003) and, finally, offspring production (Nilsen et al., 2004). Hence, while fragmented agricultural areas may appear as an attractive sink (Delibes et al., 2005), they might indeed represent the key to a higher lifetime reproductive success for those fawns surviving the hiding phase.

Figure 6. Differences among habitat types in the (a) index of visibility of fawns and (b) of mothers at the bed site; (c) index of visibility of fawns and (d) of mothers at the random site; distance between mothers and fawns in relation to the habitat type used by the fawn (e) and by the mother (f); the abundance of small rodents' species preferred by fox (SR.HAB) (e) the percentage of times a fawn was radio-monitored while active. Visibility and distances are square root transformed, in m; all parameters refer to the fawn' first month of life.



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