

Habitat and roe deer fawn vulnerability to red fox predation

M. Panzacchi^{1*†}, J. D. C. Linnell¹, M. Odden², J. Odden¹ and R. Andersen^{1‡}

¹Norwegian Institute for Nature Research, NO-7485 Trondheim, Norway; and ²Norwegian University of Life Sciences, Department of Ecology and Natural Resource Management, NO-1432 Ås, Norway

Summary

1. Notwithstanding the growing amount of literature emphasizing the link between habitat, life-history traits and behaviour, few empirical studies investigated the combined effect of these parameters on individual predation risk. We investigated direct and indirect consequences of habitat composition at multiple spatial scales on predation risk by red foxes on 151 radio-monitored roe deer fawns. We hypothesized that the higher resource availability in fragmented agricultural areas increased predation risk because of: (i) shorter prey movements, which may increase predictability; (ii) larger litter size and faster growth rates, which may increase detectability in species adopting a hiding neonatal anti-predator strategy. The sharing of risky habitat among littermates was expected to promote whole-litter losses as a result of predation.

2. The landscape-scale availability of agricultural areas negatively affected pre-weaning movements, but did not influence growth rates or litter size. Predation risk was best described by the interplay between movements and fine-scale habitat fragmentation: a higher mobility increased the encounter rate and predation risk in highly fragmented home ranges, while it reduced predation risk in forest-dominated areas with clumped resources because of decreased predictability. This is one of the first demonstrations that movement patterns can be an efficient anti-predator strategy when adjusted to local conditions.

3. In accordance with previous studies documenting the existence of family effects (i.e. non-independence among siblings) in survival, littermates survived or died together more often than expected by chance. In addition, our study specifically demonstrated the occurrence of behaviourally mediated family effects in predation risk: after a fox killed one fawn the probability of a sibling being killed within a few days rose from 20% to 47%, likely because of the win-stay strategy (i.e. return to a previously rewarding site) adopted by the predator. Hence, the predator's hunting strategy has the potential to raise fawn mortality disproportionately to predator abundance.

4. There is increasing evidence that fawns inhabiting highly productive predator-free habitats are granted lifetime fitness benefits; these potential advantages, however, can be cancelled out when predation risk increases in the very same high-productivity areas, which might thus turn into attractive sinks.

Key-words: *Capreolus capreolus*, cost of movements, landscape ecology, *Vulpes vulpes*

Introduction

Classical predator–prey models stand on the assumptions that individuals are equal, independent and move randomly in a homogeneous space (Akçakaya, Arditi & Ginzburg 1995). As these conditions are rarely met in natural ecosystems, classical models often fail to adequately portray the complexity of predator–prey dynamics (Abrams & Ginzburg

*Correspondence author. E-mail: manuela.panzacchi@nina.no

†Present address: Norwegian University of Life Sciences, Department of Ecology and Natural Resource Management, NO-14342 Ås, Norway.

‡Present address: Museum of Natural History and Archaeology, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway.

2000). Hence, a major challenge for current research is to understand the underlying mechanisms that cause violations of these assumptions, and to incorporate realistic measures of individual heterogeneity in predator–prey models (Kauffman *et al.* 2007). In this regard habitat heterogeneity could be crucial, as it is widely acknowledged as one of the major determinants of the variability in individual performance and behaviour. Furthermore, the sharing of the same habitat among related individuals promotes a violation of the assumption of independence among individuals in life-history traits and survival (Gaillard *et al.* 1998; Bishop, White & Lucas 2008). In this paper, we investigate (i) the link between habitat heterogeneity and individual differences in life-history traits, non-independence among related individuals and non-random movements of 151 radio-monitored roe deer *Capreolus capreolus* fawns, and (ii) the effect of these factors on predation risk by red foxes *Vulpes vulpes*.

The study was carried out along an environmental gradient in south-eastern Norway where we have previously shown that red foxes represent the major mortality cause for neonatal fawns accounting for 63% of all losses throughout the study area (Panzacchi *et al.* 2008a), although the role of fawns in fox diet is somewhat less important (Panzacchi *et al.* 2008b). In the southern, fragmented and more productive agricultural area predation rates were higher (25%) compared with the northern forest-dominated part (13%) of the study area (Panzacchi *et al.* 2008a). The higher predation rate has been attributed for the most part to an approximately 26 times higher density of roe deer in the southern part of the study area, which induced a more marked degree of fox feeding specialization on fawns (Panzacchi *et al.* 2008a). In addition, a three times higher abundance of foxes in the southern area likely contributed to the observed pattern (see Kjellander & Nordström 2003; Jarnemo & Liberg 2005). However, habitat heterogeneity was also hypothesized to account for a relevant part of the observed variation in predation rates for two main reasons. First, a higher abundance of roe deer (Hewison, Vincent & Reby 1998; Bunnefeld *et al.* 2006) and foxes (Kurki *et al.* 1998) in fragmented agricultural areas is a common finding largely determined by the great diversity and abundance of food items associated with forest-farmland ecotones (Andrén 1994). Second, a higher predation risk by searching predators in the open habitat seems to be a universal feature for deer adopting a hiding type neonatal anti-predator strategy (Beale & Smith 1973; Carroll & Brown 1977; Barret 1981; Aanes & Andersen 1996; Canon & Bryant 1997; Kjellander *et al.* 2004; Rohm, Nielsen & Woolf 2007). As the hiding strategy is believed to have evolved to decrease predation risk in habitats with an abundance of cover (Lent 1974), the most quoted explanation for this finding is a higher visibility of fawns and of their mothers in open habitats (Byers & Byers 1983; Fitzgibbon 1993; Jarnemo 2004a; Panzacchi 2007). Here we aim to further explore mechanisms through which habitat heterogeneity can affect neonatal predation risk.

Roe deer are long-term hiders, as the fawns hide motionless, odourless, with a reduced metabolic rate and secluded

from their mothers most of the time during their first 6–8 weeks of life. Activity is generally assumed to be dangerous for prey (Werner & Anholt 1993; Lima 1998), and this should be particularly evident in hider species at the stage when fawns are unable to escape predators (Jackson, White & Knowlton 1972; Shwede, Heindrichs & Wemmer 1992). Hence, any factor that enhances activity and detectability should be avoided. The *growth-mortality hypothesis* states that individual differences in metabolic rates, due for example to differences in energy intake, encourage differences in personality traits such as boldness, activity levels and reactivity that contribute to growth-mortality trade-offs related to risk-taking behaviour (Stamps 2007). We suggest that while species adopting and following anti-predator strategy would benefit from a higher growth rate allowing the young to better follow the mother, hiders should benefit by minimizing factors leading to higher activity levels and detectability. Habitat quality can enhance milk yields (Smith, Robbins & Anderson 1997), growth rates (Pettorelli *et al.* 2001, 2002, 2005) and litter size (Nilsen, Linnell & Andersen 2004; McLoughlin *et al.* 2007; Miyashita *et al.* 2008). As growth rates (Stamps 2007) and litter size (Pettorelli & Durant 2007) can affect predation risk, we hypothesize that the fitness benefits of living in productive agricultural areas translate into higher activity and detectability that increase predation risk from searching predators (*Hypothesis H₁*).

We also test for an effect of habitat heterogeneity on predation risk through altered movement patterns. The *predator–prey shell game hypothesis* (Mitchell & Lima 2002) proposes that prey move frequently among feeding areas to decrease their predictability to searching predators. As the high activity concentrated around agricultural patches would render roe deer particularly predictable to searching predators, we hypothesize that fawns with higher movement rates suffer lower predation risk (*H₂*). As scale is a key-determinant of the strength of the ecological patterns and processes observed (Bowyer & Kie 2006), and previous authors suggested that landscape-scale habitat characteristics may be more important to fawn survival than fine-scale habitat (Vreeland, Diefenbach & Wallingford 2004; Gustine *et al.* 2006), we tested for these hypotheses at multiple spatial scales, in an attempt to contribute to the development of the *behavioural ecology of ecological landscapes* proposed by Lima & Zollner (1996).

Finally, as twins and triplets share the same habitat and often comprise a large proportion of the data sets used to investigate neonatal survival in ungulates, we focus on the widespread issue of the violation of the assumption of independence among individuals in life-history traits and survival. Siblings are not independent individuals because of genetic effects (Wilson *et al.* 2005), maternal effects (Reinhold 2002), environmental effects (Ridley 2007) and litter effects (Pettorelli & Durant 2007). As a consequence, littermates tend to exhibit similar pre-weaning movement and activity patterns (Lent 1974), grow with similar rates (Gaillard *et al.* 1998) and survive or die as a unit (Bishop *et al.* 2008). This phenomenon, hereafter generically termed *family*

effect (*sensu* Gaillard *et al.* 1998), has been well recognized in birds (Ricklefs 1969) and it is receiving increasing attention in studies of mammals as it has the potential to increase the variance in reproductive success among females with potential repercussions on population dynamics (Swenson *et al.* 1997; Gaillard *et al.* 1998; Pettorelli & Durant 2007). The existence of family effects in survival of roe deer fawns has been previously documented in predator-free environments, and it has been putatively attributed to maternal characteristics (Gaillard *et al.* 1998). Here, we test for the existence of family effects in roe deer fawn survival (H_3) and, specifically, in predation risk by red foxes (H_4), as we hypothesize the existence of a behaviourally mediated role in generating non-independence in predation risk among siblings.

Materials and methods

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 (Fig. 1). The area encompasses a latitudinal gradient in climatic conditions and landscape 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-scaled mosaic of agricultural areas (24%), water

(11%) and forests (65%); the climate is milder and the snow cover is less persistent compared with the northern area.

The southern part of the study area supported a much higher abundance of roe deer compared with the northern area, which was partly accounted for by a marked gradient in proportion of agricultural areas and in snow cover. Red foxes were the main predators for roe deer fawns, and a wide-scale snow track count study indicated that their abundance was three times higher in the southern compared with the northern part of the study area (Panzacchi *et al.* 2008a). Red fox abundance was also positively affected by fragmented agricultural areas at several spatial scales (Panzacchi 2007; see also Kurki *et al.* 1998). Eurasian lynx (*Lynx lynx*) were abundant in the area, but only killed radio-monitored fawns on rare occasions (Nilsen *et al.* 2009a); transient wolves (*Canis lupus*) were also present but never preyed upon radio-monitored fawns.

CAPTURE AND RADIO-MONITORING OF ROE DEER FAWNS

A total of 151 fawns (76 ♂, 71 ♀, 4 unknown sex), belonging to 83 different family groups (i.e. a doe with its offspring during a given year), were captured soon after birth and equipped with expandable radio-collars. The fawns were captured by stalking radio-collared does or by spotting fawns suckling unmarked does seen by chance. As the distance between siblings during the first weeks of life is usually < 50 m (Panzacchi 2007), when only one fawn was captured we conducted repeated searches in the surrounding area in order to find littermates. All fawns were weighed at capture and in 61 cases 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. Causes of death were assessed in the field or at the Norwegian Veterinary Institute, Oslo.

STATISTICAL PROCEDURES

Direct and indirect effects of habitat on predation risk

First, we investigated the existence of direct effects of landscape characteristics on predation risk. Then, we tested for possible indirect effects of habitat on predation risk through altered growth rates and litter size (*Hypothesis H₁*), and movement patterns (H_2). For these analyses we used two indices of landscape characteristics: the proportion of fields with respect to forest, $PROP.FIELD$, calculated as (field area/[forest + field] areas), and an index of landscape fragmentation, $FRAGM$, calculated as ([field + forest edges]/area unit). Direct and indirect effects of landscape characteristics on predation risk were investigated within four concentric buffers centered in the geometric centre of activity of each family group (Fig. 1). The activity centre was identified with geographic information systems (GIS, www.gis.com) by using radiolocations collected during the period when fawns are susceptible to fox predation, which, in our study area, occurred up to 56 days of life. 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 to calculate a home range and to investigate habitat choices. The use of buffers allowed us to overcome this problem by associating predation events to habitat characteristics in the area surrounding the birth-place. The smallest buffer, hereafter termed *home range buffer*, represented the area potentially available to each family group, and was built with a radius equalling the one of the average 95% minimum convex polygon. As the home ranges were smaller in the southern part of the study area (\bar{x} = 36.2 ha, 95% confidence interval or CI,

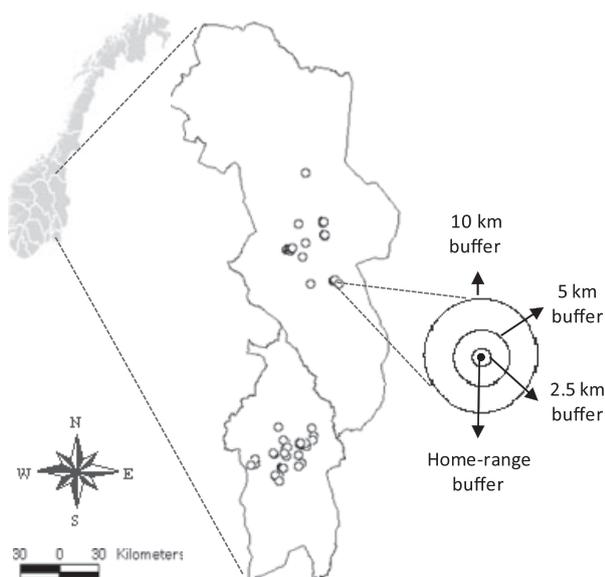


Fig. 1. Location of the study area in Norway (left) – comprising a northern subarea (i.e. Hedmark county) and a southern subarea (i.e. Østfold and Akershus counties) – and study design (right). Each dot represents the centre of activity of one radio-monitored roe deer family group. The study was carried out by adopting a multi-scale approach, and landscape characteristics were investigated in the area surrounding each activity centre within concentric buffers with radii 10, 5, 2.5 km, and within a buffer with a radius equal to the average summer home range.

lower bound: 29.2, upper bound: 49.3, $n = 36$) compared with the northern one ($\bar{x} = 146.8$ ha, lower bound: 90.6, upper bound: 203.0, $n = 22$; Mann–Whitney, $U = 125$, $P < 0.001$), we built buffers with two different radii (396 m south and 804 m north). Three additional concentric buffers of 2.5, 5 and 10 km radii represented the surrounding landscape potentially influencing the behaviour and the life-history traits of each family group. Forest fragmentation by agricultural areas in the largest buffers represented a general measure of the covariation between habitat characteristics and deer and fox abundance (Panzacchi 2007). As the resting metabolic rates of roe deer fawn increase linearly during the first month of life, and are highly correlated with body mass (Mauget, Mauget & Sempère 1999), we used individual growth rates as proxies of activity levels.

All analyses were conducted in R 2.7.0 (<http://www.r-project.org>). The relationships between landscape characteristics, fawn movements (MOVEMENT, i.e. the average distance moved between consecutive locations), litter size and growth rates were investigated using Generalized Linear Models (GLMs). As climatic conditions during spring are potentially major determinants of growth rates (Gaillard, Delorme & Jullien 1993), we tested for the effect of precipitation and temperature (<http://retro.met.no>) in April (as most of the foetal growth takes place during the last part of the gestation period) and May (as climatic conditions affect the time of spring flush, and thereby the availability of high-quality forage). In order to investigate the relationship between MOVEMENT and habitat characteristics, we performed a GLM with a negative binomial error structure to account for overdispersion. Whenever the analyses required controlling for the effect of the year, the study area (AREA) or the identity of the family (FAM), as specified in the result section, we used Linear Mixed Effect models (lmer procedure in R) considering the appropriate variable as a random effect (see Gillies *et al.* 2006). Logistic regression models have been widely used for testing hypotheses related to the spatial distribution of the risk of predation (see Kristan & Boorman 2003; Hebblewhite, Merrill & McDonald 2005). Accordingly, we investigated possible direct and indirect effects of spatial heterogeneity (i.e. habitat characteristics, litter size, growth rates and MOVEMENT) on the risk of predation by using GLM with a binomial error structure (response variable: killed/not killed). Each time it was required to account for FAM or year as random effects – as specified in the ‘Results’ section – we used the lmer procedure in R. Given the existence of family effects in survival and differences between the northern and southern parts of the study area (see Results), in order to find the best model describing predation risk we organized the data hierarchically with FAM as a random factor nested in AREA, and performed a multi-level hierarchical model (Hox 2002).

Model selection was based on the Akaike Information Criterion corrected for small samples (AIC_c). When comparing lmer models, the log-likelihood was maximized. Models with $\Delta AIC_c < 2$ were considered worthy of consideration, and their relative difference in performance was given by the normalized likelihood of the models (Akaike weights, ω_i ; Burnham & Anderson 2002). The performance of the most parsimonious models was compared with that of the null model (i.e. containing only the intercept).

Family effects on survival and predation risk

First, following Gaillard *et al.* (1998), we tested for family effects on fawn survival (*Hypothesis H₃*) by comparing the observed and the expected frequency distribution of families in which all fawns had the same fate (i.e. with family effects) with that of families in which the fawns had different fates (i.e. without family effects). Survival probabilities were calculated as the proportion of individuals that survived

for twins (S_w) and for triplets (S_t). For twins, the families were distributed among types according to a binomial distribution, while for triplets the families were distributed according to a multinomial distribution. 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 of twins and triplets is given as follows.

For twins:

$$P_{aa} = S_w^2,$$

$$P_{dd} = (1 - S_w)^2,$$

$$P_{a,d} = 2S_w(1 - S_w).$$

For triplets:

$$P_{aaa} = S_t^3,$$

$$P_{ddd} = (1 - S_t)^3,$$

$$P_{a,a,d} = 3S_t(1 - S_t)^2,$$

$$P_{a,dd} = 3S_t^2(1 - S_t).$$

The number of families expected to belong to each of the above-mentioned categories was obtained by multiplying each probability by the total number of families sampled in each subset. Hence, we tested for the null hypothesis H_{3a} that fawns belonging to the same family group had a similar probability of surviving or dying ($P_{dd} + P_{aa} + P_{ddd} + P_{aaa} > P_{ad} + P_{aad} + P_{add}$). Only families composed of twins or triplets whose fate at the end of the study period was known (i.e. either alive or dead) were considered in these analyses. As predation was a relevant mortality cause in our study area, we also tested for this hypothesis by excluding a subset of families that experienced predation (H_{3b}) to ascertain the existence of family effects in survival as Gaillard *et al.* (1998) found in predator-free areas.

Afterwards, we specifically tested for family effects on the risk of predation by foxes, i.e. we tested for the null hypothesis H_4 that the probability of observing a family in which either all fawns or two out of three fawns were killed by the fox was higher than the probability of observing a family in which one fawn out of two, or two fawns out of three survived ($H_{02}: P_{dd} + P_{ddd} + P_{dda} > P_{ad} + P_{aad}$). For this analysis, we used a sample of families composed of twins or triplets whose fate at the end of the study period was either ‘alive’ or ‘killed by fox’ (we excluded families with fawns that died for causes other than fox predation, or whose cause of death was unknown). The expected and observed values were compared using a chi-square.

Results

EFFECT OF LANDSCAPE CHARACTERISTICS ON PREDATION RISK

The home range buffers included 3.2 times more edge (Wilcoxon, $W = 6393$, $P < 0.001$) and 2.9 times more fields ($W = 5162$, $n = 81$, $P < 0.001$) compared with the

Table 1. Logistic regression models describing roe deer fawn predation risk with respect to landscape characteristics. Dependent variable: individual fawns (i.e. killed by fox vs. alive; $h = 138$) or family groups (i.e. at least one member of the family group killed vs. all members alive; $n = 69$); $k = 2$. Fixed factors: proportion of fields with respect to forest (PROP.FIELD), and forest fragmentation by agricultural areas (FRAGM) within four concentric buffers of different radii (2.5, 5 and 10 km), the smallest representing roe deer fawn's home range (HR)

Landscape characteristics	Scale	Individual predation risk			Predation risk in family groups		
		ΔAIC_c	ω_i	P	ΔAIC_c	ω_i	P
PROP.FIELD	10 km	2.914	0.111	*	4.119	0.067	
	5 km	4.279	0.056		3.896	0.075	
	2.5 km	5.489	0.031		4.232	0.064	
	HR	5.626	0.029		4.386	0.059	
FRAGM	10 km	3.906	0.068		3.784	0.079	
	5 km	2.538	0.134	*	3.898	0.075	
	2.5 km	5.876	0.025		4.559	0.054	
	HR	0.000	0.477	**	0.000	0.527	**
Null model		3.825	0.070		2.190	0.176	

Best performing models are given in bold characters. Significance codes: * $P < 0.07$ and ** $P < 0.05$.

surrounding 10 km. The difference in PROP.FIELD was particularly marked in the northern part of the study area (18.3 vs. 2.7 times, respectively). Table 1 illustrates the relationship between predation risk, PROP.FIELD, and FRAGM at different spatial scales. Among the candidate models, the probability of a fawn being killed by a fox was best described by FRAGM within the home range (GLM, slope on a logit scale = 91.460 ± 38.631 SE, $Z = 2.368$, $P = 0.018$). This result was consistent even when considering predation risk within each family group as a dependent variable (98.415 ± 47.784 , $Z = 2.060$, $P = 0.039$).

HABITAT EFFECTS ON LITTER SIZE AND PREDATION RISK

Fawns were captured on average 5.9 ± 5.5 SD ($n = 151$) days after birth, without differences between the northern and southern parts of the study area (t -test, $t = 1.287$, d.f. = 54.451, $P = 0.204$). The observed litter size at capture (1.9 ± 0.7 , $n = 81$) was probably underestimated because of

the occurrence of mortality before capture for the most part due to red foxes. In fact, the age at capture was negatively correlated with predation risk (GLM, $Z = -2.026$, d.f. = 121, $P = 0.043$), to the probability of a fawn belonging to a triplet ($Z = -2.804$, d.f. = 80, $P = 0.037$) and, in general, tended to be inversely related to litter size ($t = -1.673$, d.f. = 80, $P = 0.098$). When accounting for the age at capture, we detected a negative relationship between litter size and the PROP.FIELD in the surrounding 10 km (lmer, estimate = -1.309 ± 0.510 SE, $t = -2.567$, $P = 0.013$; Table 2). However, predation risk was not related to litter size ($Z = 0.360$, d.f. = 80, $P = 0.718$).

HABITAT EFFECTS ON GROWTH RATES AND PREDATION RISK

The average growth rate (155 g day^{-1} , 95% CI: 146–163, $n = 59$) was not affected by SEX (males: 0.157 g day^{-1} , CI: 144–170, $n = 23$; females: 0.150 g day^{-1} , CI: 138–162, $n = 36$; $t = 0.906$, $P = 0.240$), year ($F = 1.481$, d.f. = 51,

Table 2. Effect of landscape characteristics (see Table 1) on roe deer litter ($n = 81$) size, index of individual ($n = 145$) movements and index of family ($n = 75$) movements. As the observed litter size was higher for fawns captured soon after birth, the effect of habitat on litter size was investigated by using Linear Mixed Effect models with the age at capture as random effect. The effect of landscape characteristics on movements was investigated by using Generalized Linear Models

Landscape characteristics	Scale	Litter size			Individual movements			Family movements		
		ΔAIC_c	ω_i	P	ΔAIC_c	ω_i	P	ΔAIC_c	ω_i	P
PROP.FIELD	10 km	0.000	0.618	*	43.693	0.000	**	24.499	0.000	*
	5 km	5.436	0.041		13.328	0.001	**	9.392	0.008	**
	2.5 km	6.421	0.025		0.000	0.955	**	0.000	0.901	**
	HR	6.025	0.030		22.613	0.000	**	8.843	0.011	**
FRAGM	10 km	9.089	0.007		64.716	0.000		32.836	0.000	
	5 km	4.386	0.069		6.186	0.043	**	5.487	0.058	**
	2.5 km	5.976	0.031		17.770	0.000	**	8.744	0.011	**
	HR	3.500	0.107		21.093	0.000	**	8.800	0.011	**
Null model		4.297	0.072		62.705	0.000		30.910	0.000	

Best performing models are given in bold characters. Significance codes: * $P < 0.05$ and ** $P < 0.001$.

7, $P = 0.195$), AREA (south: 0.155 g day^{-1} , CI: $0.140\text{--}0.175$, $n = 33$; north: 0.154 g day^{-1} , CI: $0.141\text{--}0.166$, $n = 26$; $t = 0.260$, $P = 0.796$) or litter size (single fawn: 0.157 g day^{-1} , CI: $0.140\text{--}0.175$, $n = 6$; siblings: 0.156 g day^{-1} , CI: $0.142\text{--}0.169$, $n = 30$; triplets: 0.152 g day^{-1} , CI: $0.136\text{--}0.169$, $n = 23$; $F = 0.168$, $P = 0.683$). However, we detected family effects in growth rate, as its variability within each family group was lower compared with that between family groups ($F = 3.546$, d.f. = 27, 21, $P = 0.002$). When accounting for this factor, we did not detect any significant relationship between growth rates and climatic or environmental variables, as the ΔAIC_c of the best performing lmer models was higher than that of the null model. Contrary to our expectations, we did not detect any relationship between growth rates and predation risk (GLM, $t = 0.890$, d.f. = 35.047, $P = 0.380$), even when accounting for FAM (lmer in R, $Z = -0.367$, $P = 0.713$) or the year ($Z = -1.123$, $P = 0.262$). We tested for differences in predation risk among 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 killed by a fox (Wilcoxon, $Z = -0.119$, $P = 0.906$).

HABITAT EFFECTS ON MOVEMENTS AND PREDATION RISK

Mortality (GLM, $Z = 0.248$, d.f. = 146, $P = 0.804$) and predation risk ($Z = -1.091$, d.f. = 127, $P = 0.275$) were not sex-biased. However, we tested for a possible indirect effect of sex on predation risk through altered movement patterns. In the first 56 days of life, individual MOVEMENT differed greatly between the southern ($\bar{x} = 265 \pm 224 \text{ mSD}$, $n = 1171$) and northern parts of the study area ($\bar{x} = 530 \pm 450 \text{ m}$, $n = 568$; $t = 19.267$, d.f. = 1417, $P < 0.001$). However, within each family group, MOVEMENT did not increase significantly with age (lmer, value = 1.001, SE = 0.644; $t = 1.563$, $P = 0.118$), nor was it affected by sex (value = -21.932 , SE: 21.336; $t = -0.948$, $P = 0.343$). Contrary to our expectations, MOVEMENT was not affected by growth rates, when controlling for FAM ($t = 0.645$, d.f. = 26, $P = 0.525$). MOVEMENT was negatively affected by forest fragmentation by agricultural areas at most spatial scales, with the best relationship occurring at the 2.5 km buffer scale (GLM, estimate for individual fawns $-1.952 \pm 0.223 \text{ SE}$, $t = -8.741$, $P < 0.000$; estimate for family groups: $-1.847 \pm 0.289 \text{ SE}$, $t = -6.400$, $P < 0.000$; Table 2). Predation risk was negatively affected by MOVEMENT both considering the individuals ($Z = -2.357$, d.f. = 118, $P = 0.018$) or the family group ($Z = -2.095$, d.f. = 63, $P = 0.036$) as a unit.

In Table 3, we present the five best performing models explaining predation risk, with FAM as a random factor nested in AREA. The most parsimonious model included the interaction MOVEMENT*FRAGM within each home range ($4.821 \pm 3.630 \text{ SE}$, $Z = 1.328$; Table 3 and Fig. 2). In the more forest-dominated areas predation risk was highest for fawns that only moved short distances while on the contrary, in fragmented

Table 3. Set of five best performing Generalized Linear Mixed Effect models explaining individual predation risk (i.e. preyed upon or not) with the family identity, FAM, as a random factor nested in AREA. The models used for comparison had the following fixed factors: (i) the distance between consecutive locations (MOVEMENTS); (ii) the proportion of fields with respect to forest (PROP.FIELD) or landscape fragmentation (FRAGM) within 10, 5 and 2.5 km or within the home range (HR); (iii) the sum or the interaction between MOVEMENTS and PROP.FIELD or FRAGM within the HR or within the 10 km buffer. The most parsimonious model is on top of the list

Model	ΔAIC_c	ω_i	k
MOVEMENTS * FRAGM HR	0.000	0.831	6
MOVEMENTS * PROP.FIELD HR	3.721	0.129	6
MOVEMENTS * PROP.FIELD 10 km	7.867	0.016	6
MOVEMENTS	8.024	0.015	4
MOVEMENTS + FRAGM HR	9.260	0.008	5
Null model	14.020	0.001	3

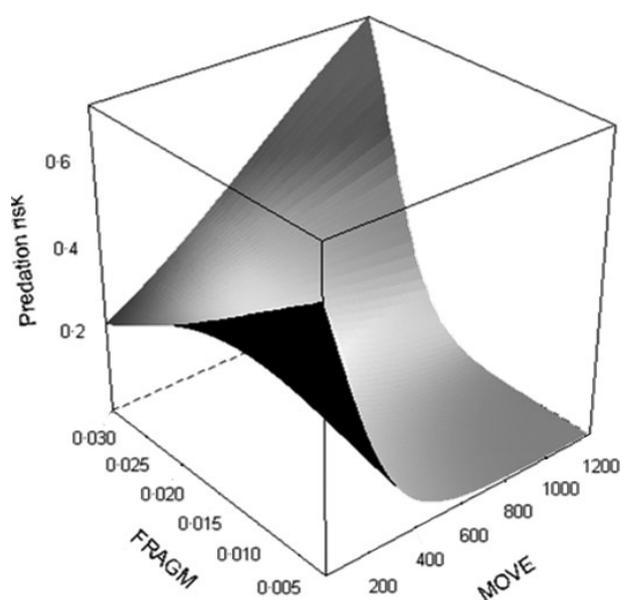


Fig. 2. Relationship between roe deer fawn predation risk by red foxes in south-eastern Norway with the distance moved between consecutive locations (MOVEMENT) and the index of habitat fragmentation (FRAGM) within the home range buffer, as indicated by the most parsimonious model presented in Table 3.

agricultural areas, predation risk was highest for fawns with a higher mobility.

FAMILY EFFECTS IN SURVIVAL AND IN PREDATION RISK

We detected the occurrence of family effects in survival, as fawns belonging to the same family group ($n = 53$) had a similar probability of surviving or dying (*Hypothesis* H_{3a} , $\chi^2 = 4.598$, d.f. = 1, $P = 0.032$) because of all known mortality causes. However, this finding was largely affected by the occurrence of predation, as it was no longer significant when excluding those family groups that experienced predation (H_{3b} , $\chi^2 = 2.851$, d.f. = 1, $P = 0.091$, $n = 41$ fami-

lies). Indeed, when considering only those family groups that experienced predation, the probability of observing families in which the majority of fawns were killed by fox was higher than expected under the null hypothesis H_4 of no family effects in predation risk ($\chi^2 = 4.187$, d.f. = 1, $P = 0.041$, $n = 41$ families). The overall predation rate was 20%, i.e. red foxes killed 1 out of 5.1 fawns ($n = 143$). However, when considering a subsample of families ($n = 12$) composed of fawns ($n = 27$) either alive or killed by the fox at the end of the study period, the situation changed: after one sibling was killed by the fox, 1 out of 2.1 of the remaining siblings were killed too. Hence, predation risk for the remaining siblings rose from 20% to 47%. 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.

Discussion

This study demonstrates that neonatal predation risk of polytocous ungulates can be affected by habitat-specific movement patterns, and can be enhanced by the hunting strategy adopted by a predator. Pre-weaning movements are primarily driven by the particularly high energetic constraints of the roe deer does (Andersen *et al.* 2000), which search for high-quality forage granting high fitness benefits for both the doe and fawns (Pettorelli *et al.* 2001, 2002). In particular, recent studies have shown that both roe deer (McLoughlin *et al.* 2007) and sika deer (*Cervus nippon*; Miyashita *et al.* 2008) mothers select farmlands and field-forest edges in order to increase their reproductive success. In keeping with the theory that ranging movements decrease as resource availability increases (Geist 1982; see also Saïd *et al.* 2005), we found that mobility was negatively affected by the proportion of agricultural areas at most spatial scales, with the strongest relationships occurring within 2.5 and 5 km. Hence, the decision on how to move through the landscape seems to be based upon information referring to a much larger spatial scale compared with that actually used by the family group (i.e. a few hundreds of metres) in its day-to-day activity. The discrepancy between the *perceptual range* (cf. Lima & Zollner 1996) and the fawning range may leave a margin for possible anti-predator adjustments of the foraging strategy (see Gustine *et al.* 2006). Not only did roe deer strongly select home ranges with a high proportion of agricultural areas but, also, concentrated their activity in close proximity to the field edges (see Tufto, Andersen & Linnell 1996; Panzacchi 2007). As expected, restricted movements in the proximity of spatially clumped resources increased the predictability of the location of the fawn and, consequently, its predation risk. However, the effect that movements had on predation risk differed markedly depending on the availability and spatial distribution of resources (H_2 was partially supported). In fragmented agricultural home ranges with lots of farmland and with a higher prey and predator density (Panzacchi 2007), a reduced mobility decreased the encounter rate, detectability and predation risk (see Ozoga & Verme 1986). On the contrary, in

forest-dominated home ranges short movements concentrated around the few agricultural fields remarkably increased the predictability of fawn location and predation risk (Fig. 2; see Lima & Dill 1990; Byers 1997; Mitchell & Lima 2002). To our knowledge, this is one of the first empirical demonstrations that mobility can function as an effective anti-predator behaviour (see Gustine *et al.* 2006), and strongly supports the *predator-prey shell game theory* proposed by Mitchell & Lima (2002), i.e. that predators attempt to learn prey location while prey attempt to be unpredictable. According to the simulations performed by Mitchell & Lima (2002), the best strategy for prey depends on the behaviour of the predator: non-learning predators favour non-moving prey, while learning predators favour moving prey. Our results demonstrate that this theory can be discussed from a predictability point of view: for a given predator species, a non-predictable distribution of resources will favour non-moving prey, while predictable resources favour moving prey.

Several lines of evidence suggest that fragmented agricultural areas, in particular meadows and field-forest edges, support a high availability of high-quality trophic resources (e.g. Miyashita *et al.* 2008 and references therein; McLoughlin *et al.* 2007). Contrary to our expectations, we found no relationship between the availability of fragmented agricultural areas and life-history parameters such as growth rates or litter size (H_1 was not supported). We also failed to find any effect of growth rate or litter size on predation risk. Note, however, that litter size was underestimated likely because of predation occurring before capture, and our results strongly suggest that this undetected predation occurred mainly in the most productive areas. As there are an increasing number of studies demonstrating a link between spatial distribution of resources and fitness components (Pettorelli *et al.* 2001, 2003; Nilsen *et al.* 2004; McLoughlin *et al.* 2007; Miyashita *et al.* 2008), it is possible that we simply failed to describe the relevant drivers affecting variation in growth rates and litter size. However, as all studies cited before refer to predator-free areas, we cannot exclude the hypothesis that in our study the potential energetic benefits of living in more productive agricultural areas were traded-off against the higher predation pressure in the same habitats. Possible mechanisms involved in this process may be increased mother vigilance to the detriment of foraging (e.g. Wolff & Van Horn 2003), reduced mother-fawn interactions or reduced milk-suckling rate to limit detectability to sit-and-wait predators such as red foxes (Jarnemo 2004b).

Littermates survived or died together more often than expected by chance. The non-independence among siblings in survival disappeared when removing the effect of predation (i.e. H_3 was only partly supported), but this result might be affected by the reduced sample size of families with fawns that died only for reasons other than predation. However, we detected marked family effects in the risk of a roe deer fawn being killed by red foxes (i.e. H_4 was supported). After a fox killed one member of a family group, the probability of a sibling being killed rose from 20% to 47%. Despite the wide-

spread anecdotal evidence that some predators tend to kill whole litters (Schaller 1972; Pettorelli & Durant 2007; Bishop *et al.* 2008), this demonstration of the existence of family effects in predation risk is, to our knowledge, a novel finding in polytocous mammals with potentially relevant consequences for population dynamics. Indeed, in predator-free areas the non-independence among siblings in survival caused a threefold increase in the variance in lifetime reproductive success among females (Gaillard *et al.* 1998). If predation does not act independently on siblings, we expect a further increase in the variance in reproductive success among females. We encourage other studies to investigate the occurrence of family effects in predation risk in other predator-prey systems and their potential effect on population dynamics. The available evidence suggests that family effects in survival are widespread in polytocous mammals (Boutin, Roses & Caley 1988; Gaillard *et al.* 1998; Pettorelli & Durant 2007; Bishop *et al.* 2008). However, their magnitude can be either limited (Bishop *et al.* 2008), significant only during unfavourable environmental conditions (Gaillard *et al.* 1998), or strong (Pettorelli & Durant 2007). We suggest that the causes of this variability might be related to the reasons underlying the observed effects. In predator-free areas the dependence among siblings is likely to be entirely attributed to the mothers' attributes and, thus, it increases with environmental harshness (Gaillard *et al.* 1998). However, when predation is a relevant mortality factor the magnitude of the family effects may either be enhanced or reduced by the functional response and hunting strategy of the predator. If predation acts independently on siblings because of random predator searching strategies and/or mother-neonate behavioural adaptations, predation may level out the effect of biological and environmental variables inducing dependence in survival among littermates (see Bishop *et al.* 2008) and reduce the variability in female reproductive success. On the contrary, if the predator kills all littermates at once (e.g. infanticide, Swenson *et al.* 1997) or adopts a *win-stay hunting strategy* (i.e. returns to a previously rewarding location, Olton, Handelmann & Walker 1981), predation may increase the magnitude of family effects with potential consequences on population dynamics. Although foxes are capable of multiple killings (e.g. Sonerud 1985), in only two cases were roe deer siblings killed in the same attack, as a few days normally elapsed between consecutive predation events; a similar time lag was recorded in coyote *Canis latrans* predation on mule deer *Odocoileus hemionus* fawns (Bishop *et al.* 2008). This supports the finding that roe deer does play an important role in deterring the predator from consecutive attacks on hiding offspring (Jarnemo 2004b) and, most importantly, indicates that foxes memorize successful hunting sites and return to kill the surviving littermates. The win-stay hunting strategy has been documented in foxes, weasels (*Mustela nivalis*) and in several birds of prey (Sonerud 1985), and it is an efficient hunting tactic for exploiting clumped prey that only move short distances (Mitchell & Lima 2002). Roe deer twins and triplets are, indeed, clumped prey that move relatively short distances, relative to the scale at which red foxes use the land-

scape. Movements are one of the most important parameters explaining predation risk in this study.

In conclusion, our study provides empirical evidence of the effect of habitat producing heterogeneity in predator-prey dynamics by altering prey movement patterns and supporting non-independence among individuals in predation risk. The available evidence indicates that the higher neonatal predation risk commonly observed in open habitats (Aanes & Andersen 1996; Kjellander *et al.* 2004) is the result of a complex interaction involving factors operating at different spatial scales (Bowyer & Kie 2006). Environmental, climatic and anthropogenic variables affect predator and prey densities at a regional scale (Panzacchi 2007; see also Walström & Kjellander 1995) and, thus, determine to a great extent the predator's functional response and the overall predation rates and patterns (Panzacchi *et al.* 2008a). At smaller landscape scales the abundance and distribution of resources determines movement patterns, which can have great consequences on predation risk in a way determined by the fine-scale ecological settings of the home range, increasing it where resources are abundant and widespread and decreasing it where resources are scarce and predictable. Finally, at a given time and place, the probability of a fawn being killed by a red fox can be further affected by vegetation characteristics affecting visibility and approachability (Panzacchi 2007; see also Van Moorter *et al.* 2009). The multiplicative effect because of the non-independence between siblings in predation risk may further contribute to the higher predation rates commonly observed in open areas. Hence, the available evidence indicates that in areas with high red fox densities fragmented agricultural areas support higher predation rates, which do not seem to be counterbalanced by larger litter size or growth rates and, thus, may represent an attractive sink (*sensu* Delibes, Gaona & Ferreras 2001). On the contrary, when predation pressure is low or absent all studies agree on the high fitness benefits of living in highly productive fawning ranges (Pettorelli *et al.* 2001, 2002; Kjellander *et al.* 2004; McLoughlin *et al.* 2007; Miyashita *et al.* 2008). These results underline the important differences that arise in life-history traits when predation pressure exists (Nilsen *et al.* 2009b).

Considering the high site fidelity commonly observed in roe deer (Linnell & Andersen 1995), the potential fitness advantages of living in areas providing high-quality forage, and the occurrence of family effects on early body development and survival, Gaillard *et al.* (1998) suggested that in predator-free areas most individuals in a stable population are descendants from only a few successful families, i.e. the ones inhabiting the best quality ranges (Nilsen *et al.* 2004). However, most roe deer populations throughout their range coexist with red foxes, and Jarnemo (2004a) showed that the reproductive success of females inhabiting agricultural habitats was highest only in years with low fox density, while the situation was reversed in years of high fox abundance. Hence, when predation is a relevant mortality it causes a trade-off between high-quality forage and predation risk may arise and, eventually, may lead to roe deer populations characterized by a higher genetic variability compared with 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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