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# Predator community and prey dynamics

*- a case study of roe deer and re-colonizing fox, lynx and wolf*

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## ABSTRACT

The role of predation is a central question in ecology and population dynamics. In South-central Sweden, the predator community has gone through drastic changes over the last fifty years with the progressive recovery of three large predators: the fox (*Vulpes vulpes*), recovering after a sarcoptic mange (*Sarcoptes scabiei*) outbreak, the lynx (*Lynx lynx*) and the wolf (*Canis lupus*), the two latter re-colonizing the region after a massive population persecution at the beginning of the 20<sup>th</sup> century. These three species potentially prey upon roe deer (*Capreolus capreolus*). Although it is one of the most common ungulate species in Europe, the combined effect of several predators on its survival is poorly documented. The objective of this study was therefore to infer how roe deer responds to the changes in a gradually increasing multi-predator system, and to estimate the consequences for population growth rate.

I used long-term (37 years) series based on telemetry data to analyze annual survival rates of 458 known-aged roe deers captured in Grimsö Wildlife Research Area (GWRA) between 1975 and 2012. Two complementary methods, the Cumulative Incidence Function and Cox Proportional Hazards were used to generate accurate estimates under a competing-risk framework. Predation was found to be largely additive to natural and human-related mortality causes, making the total mortality to increase by 40%. The compensatory or additive nature of each predation risk (fox, lynx or wolf) was unclear, but wolf is suspected to play an increasingly important role in the future. Monte-Carlo simulations with projection matrices corresponding to the four risk regimes experienced by roe deer confirmed the synergistic effect of the three predators on roe deer population growth rate as it decreased by more than 17% in the presence of the three predators, a pattern that could explain the recent drop in roe deer densities by 80% in GWRA in the 10-15 recent years.

**Key words:** *Canis lupus*, *Capreolus capreolus*, Cumulative Incidence Function, competing risks, Cox Proportional Hazards, *Lynx lynx*, population dynamics, survival analysis, *Vulpes vulpes*.

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# INTRODUCTION

Prey-predator interactions are a key component of ecological systems because of their potential impact on population dynamics (Brown *et al.* 1999), habitat selection (Creel *et al.* 2005), behaviour (Creel *et al.* 2008) and other processes like trophic cascades (Drossel *et al.* 2001) that can shape the landscape (Beschta & Ripple 2010). Beyond the natural frame, they can also have strong societal impacts because of conflicts that may arise with animal husbandry (Treves & Karanth 2003). In terrestrial systems, a predator can affect its prey in two different ways: directly by killing it, and indirectly by inducing changes in behaviour as an anti-predator response (see Creel & Christianson 2008 and Laundré 2010). As a result, individual fitness may be affected negatively and might lead to fluctuations in population growth rate. In the absence of this top-down control, food supply is believed to be the most important factor limiting ungulate population growth rate (Sinclair & Krebs 2002). However, one might question to what extent does prey population growth rate reflect the transition from a predator-free environment to a system that includes predation? Hence, what happens if several predators prey on the same species? In Scandinavia, predator community has experienced dramatic changes over the last hundred years, leading to discontinuous pressures on prey populations (Sand *et al.* 2006).

The red fox (*Vulpes vulpes*) is a very important species in the boreal ecosystem, since it is highly adaptive and able to switch prey depending on availability and environmental conditions (Kjellander & Nordström 2003). The lynx (*Lynx lynx*) used to be distributed all over Scandinavia but at the beginning of the 20<sup>th</sup> century was the population restricted to small areas between Norway and Sweden (Andrén *et al.* 2002). Since then, changes in management regimes lead to an expanding population that counted approximately 250 family groups in Sweden in 2010. The wolf (*Canis lupus*) was regarded as 'functionally extinct' in the Scandinavian peninsula in 1966; after a few reproductive events in Sweden, the population started to grow in 1991 (Wabakken *et al.* 2011) and today it represents approximately 250 individuals (Viltskadecenter, online annual publications). In Scandinavia, these three species potentially share at least one prey species: the European roe deer (*Capreolus capreolus*), a small cervid native to Sweden, whose population dynamics is expected to be sensitive to predation pressure, as recently indicated by an episode of sarcoptic mange (*Sarcoptes scabiei*) that greatly reduced the whole fox population, increased neonate roe deer survival and resulted in a peak in roe deer density (Lindström *et al.* 1994). The fox is known to be largely responsible of fawn mortality, predation rates ranging from 14% (Nordström 2010) in forested landscapes to  $\geq 40\%$  in agricultural landscapes (Jarnemo *et al.* 2004). The lynx is a roe deer specialist (Jedrzejewski *et al.* 1993) and therefore plays a very important role in its prey dynamics. It has been shown to have a clear preference towards roe deer (Molinari-Jobin *et al.* 2007), even when they occur at very low densities in areas with several alternative prey species (Odden *et al.* 2006). In the same study, Odden *et al.* (2006) argue that lynx population structure does not play a

significant role in kill rates, whereas other studies tend to prove the opposite (Molinari-Jobin *et al.* 2002). Wolf predation on roe deer seems ‘density-independent’, as roe deer in an Italian study represented the same volume in wolf scats (20%) irrespective of the roe deer density (Mattioli *et al.* 2004). Moreover, in Sweden, Olsson *et al.* (1997) showed that wolves killed roe deer three times more often than moose when compared to their relative densities.

As there is an increasing interest in multi-predator systems (Kunkel *et al.* 1999; Griffin *et al.* 2011; Gustine *et al.* 2006; Ballard *et al.* 2001; Griffen & Byers 2006), the Swedish predator-prey system could act as a perfect case study of the consequences of large predator recovery on a prey population. For example, as exploited in this paper, in Grimsö Wildlife Research Area (GWRA) the roe deer population has experienced three increasingly complex predator regimes (communities). Firstly by the return of the fox in 1990 after 8 years of depressed densities due to the sarcoptic mange outbreak, secondly the returning lynx (1996) after approximately 30 years of absence and finally during the recent nine years also the re-colonizing wolf (since 2003). However, multi-predator systems are more complex to model and require long time-series of high quality. Fortunately, at GWRA, roe deer have been equipped with radio collars for almost 40 years and new modeling tools ensure such an approach feasible (Murray & Patterson 2006; Murray 2006). Survival analysis and particularly competing-risk methods can help revealing predation patterns, and testing hypothesis of compensatory vs. additive mortalities. Additive mortality occurs when an additional cause of mortality does not change the relative importance of other causes; on the contrary, a compensatory cause of mortality is one that replaces another, thereby not affecting the total mortality (Murray *et al.* 2010). Both patterns have different consequences in terms of population dynamics. Additive mortalities are detrimental for the prey and should eventually induce changes in population growth (Melis *et al.* 2009); on the opposite, compensatory mortalities reveal competition between the predators (Griffin *et al.* 2011), forcing them to change their diet (Helldin & Danielsson 2007) or potentially reducing their numbers (Helldin *et al.* 2006).

This paper attempts to quantify the influence of predator community composition on roe deer survival by an almost 40 years long telemetry study in South-central Sweden. Such dataset also provides additional information on roe deer population features like patterns of senescence (Loison *et al.* 1999), differential annual survival between age classes or sex, and population growth rate, thereby answering the call from Murray *et al.* (2010) to use complementary methods of individual-based hazards and population-level mortalities .

According to the general patterns in ungulates, I predict that: (1) females should live longer with generally higher survival compared to males (Loison *et al.* 1999). Because natural and human-related mortalities are not supposed to be greatly affected by predation, the latter is expected to be additive to the two former ones (or at least partially-compensatory); (2) total mortality is then expected to increase with

the number of predators. However, predation does not necessarily have a uniform impact on all age and sex classes, making it quite tough to predict the synergistic effect of the three predators; (3) lynx and wolf predation is expected to be largely additive to fox predation because of the additional risk endured by other age classes than only fawns (Aanes & Andersen 1996; Jarnemo *et al.* 2004); consequently, I predict that (4) population growth rate should be higher in predator-free systems than in the presence of predators. Finally, if reproducing females experience successively decreasing survival because of increasing predation, then (5) roe deer growth rate should decrease with increasing number of predators.

## **MATERIAL AND METHODS**

### **♦ *Study area***

Grimsö Wildlife Research Area (GWRA) is located in South-central Sweden (Örebro county, 59°40' N, 15°25' E), and extends over an area of 130km<sup>2</sup>. About 70 % of that area is covered by forest (of which 74% is coniferous forest), 3% agricultural land, and the remaining 27% consists of bogs, mires, lakes and rivers. The topography is quite even, with altitudes between 75 and 180 m; for a more detailed description of GWRA, see Angelstam *et al.* (1982).

Because winter is an important factor of roe deer survival (Mysterud *et al.* 1997), a measure of winter harshness was needed in the models. The more snow on the ground, the more difficult for roe deer to find food. Therefore, to categorize winter severity, I used annual number of days with  $\geq 30$  cm of snow. Data on snow depth were obtained from the meteorological station at Ställdalen (39km North-West from GWRA, Swedish Meteorological Institute, SMHI).

### **♦ *Predators in Grimsö Wildlife Research Area***

Fox has always been present in Grimsö. However, between 1982 and 1990, the sarcoptic mange significantly reduced the fox population and the predation pressure on roe deer neonates (Lindström *et al.* 1994). The lynx first appeared in 1990 and the first reproductive event was documented in 1996. Lynx are solitary animals, with females and cubs forming family groups; they are territorial with low intra-sexual territory overlap. It is an ambush predator that stalks its prey, unlike the wolf whose predation on roe deer is rather driven by random encounters. This latter predator is the most recently settled in GWRA. In 2003, two wolves constituted the 'Uttersberg territory' partly overlapping the GWRA and had a few reproductive events between 2004 and 2007, before being replaced by the 'Hedbyn territory' completely overlapping the entire GWRA since 2009 (Viltskadecenter, online annual publications). The golden eagle (*Aquila chrysaetos*) is present in GWRA and can potentially prey on roe deer. However, eagles took only 3 roe deer (two fawns and one adult) in this study, and therefore were not categorized as a risk but merged into the stratum 'predation' (see below).

To reflect this increasing complexity in predator community, I identified four predator communities defined by the predation risk, with one predator-free community acting as a control (corresponding to the episode of sarcoptic mange, Community 1). Human-caused mortality (particularly human harvest) is encompassed in the four communities and predation risks are gradually added in the system, enlarging the risk set an individual roe deer is subject to. Community 2 adds fox predation to human and natural causes, Community 3 includes the lynx predation and Community 4 adds wolf predation. By doing this could the additive or compensatory mortality hypothesis be tested because one predator is added in each community.

♦ *Roe deer monitoring*

Since the establishment of the GWRA, roe deer population size has been fluctuating between 2 and 15 individuals per square kilometer. Annual pellet counts (Pehrson 1997) since 1976 reveal a steady decline over the last decade and the reasons for this recent decline remain unclear. The roe deer population has been monitored since the early 1970's and in 1974 was the first animal radio-collared with a VHF-transmitter. Since then, almost one thousand individuals have been followed and in recent years with GPS-collars. In this study, only known-aged animals are used to investigate survival patterns, since adult roe deer is known to be difficult to age under field conditions; this limitation thereby avoids flaws in the data set (which can be detrimental when sorting the individuals in several age classes). Animals were captured using trap boxes ( $n = 884$ ) or caught by hand in the summer as newborn. Most neonates were equipped with radio collars with an expandable strap, before they were caught again in the winter and equipped with an adult collar. All caught animals were marked with individual plastic ear-tags for recognition at later encounters; at best, it was retrieved during its first year, but some were recaptured more than one year after their first capture and this 'delayed' entry was accounted for in the models.

Eventually, 458 known-aged animals (225 males and 233 females) could be included in this 37 years study based on telemetry data (from February 1975 to February 2012). Monitoring frequency has changed through time. Ideally, individuals were followed once a week but the monitoring has been less intense for some periods, mainly during summer, with one position per month. In addition to this temporal variation in radio tracking, there is also a spatial heterogeneity in the monitoring routine as seasonal migrators were followed even less intensively if they left the study area with long distance. Such long distance migrators were usually located by aircraft and only once or twice every year in the summer range. A covariate controlling for the migratory status of these animals was therefore created.

#### ♦ *Survival analysis*

All models and tests have been carried out using statistical packages of Program R (version 2.11.1, R Foundation for Statistical Computing, Vienna, Austria). I estimated annual survival of roe deer on a daily time step. This choice was motivated by the fact that fox predation could act on the very first days of fawns' lives. The roe deer year is here assumed to start the 1<sup>st</sup> of June, as 80% of the births take place within 30 days, between mid-May and mid-June (Gaillard *et al.* 1993a). Roe deer that survived more than one year were assigned 365 as the exit date and 0 as the entry date of the consecutive year. Since these consecutive years are not independent, I used clustering to identify individuals and achieve robust variances in the models (Lin & Wei 1989). I assumed constant monitoring through the whole life of the individuals; either they left the study (because of dispersal or because reaching February 2012 alive) and were right censored (n = 152), or the animal died (carcass or collar found, n = 306).

Since the 1990-ies the radio collars have been equipped with a mortality sensor and when an indication of mortality was suspected, the location was visited by field personal as soon as possible. However, it could take several weeks before a mortality signal was detected and the possibility to infer the exact cause of death was then very low. If the animal was retrieved after death, an autopsy was performed to document the most likely cause of death. If preyed upon, the predator species was determined based on bite marks, hairs, scats and tracks as fox, lynx or wolf. When the killing predator determination was not totally clear, was the second most probable cause reported. If only the collar was found intact (i.e. drop off not activated), the cause of death was categorized as 'natural'. This will most likely be a conservative estimate of predation and several other causes as hidden predation and other unknown causes of death may be included in this category. In addition to that, drowning, disease, and starvation were also included among the 'natural death causes' stratum (n = 110). Human-related causes (n = 81) were mainly hunting, but also vehicle accidents, hay mowing, and project-induced mortalities (mortalities that are directly or suspected to be linked to the roe deer handling, e.g. animals killed to retrieve the collar or neonate fawns abandoned by the mother as a possible result of the capture process). Finally, predation was analyzed in two different ways. First, to test if predation was additive or compensatory with natural and human-related mortalities, all predations were pooled together (lynx, fox, wolf, eagle, and 'predation' when unsure about the identity of the predator, n = 115). Secondly I performed the same analysis, splitting predation in 'unknown' (and eagle) predation (n = 18), fox (n = 13), lynx (n = 72) and wolf (n = 12).

#### ♦ *Cumulative Incidence Function*

In case of multiple mortality causes (or 'fates'), simple models like the widespread Kaplan-Meier estimator are too limited, as they assume mutually exclusive and non-competing risks. Improvements of these models gave birth to the "complement of the Kaplan-Meier method" also known as the "1-KM"

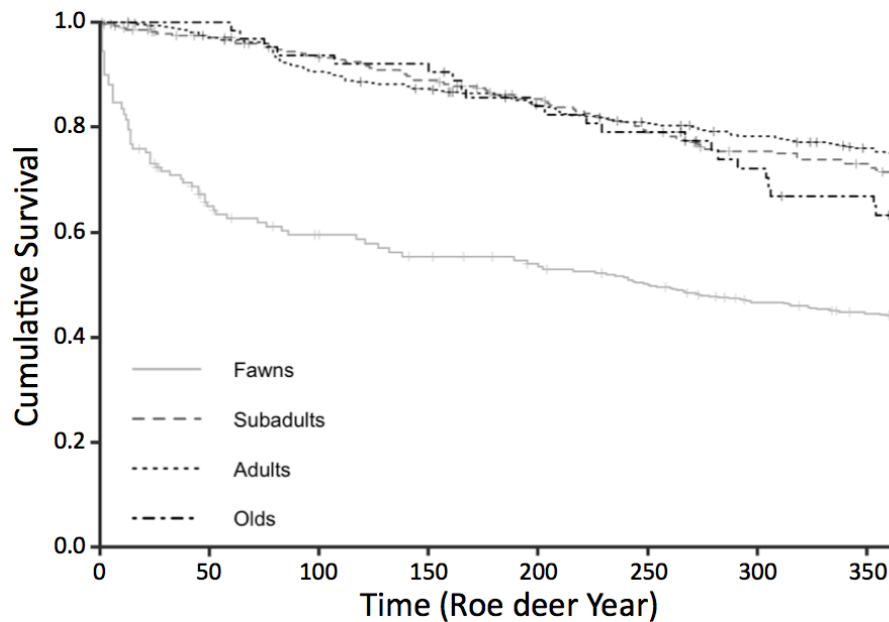
method in order to adapt the model for the competing-risks framework. However, these models are not completely accurate since they estimate each cause-specific rates in the absence of competing risks. In other words, individuals dying from a given cause are thus not available for other causes. Recently, Heisey and Patterson (2006) developed an estimator based on the Cumulative Incidence Function (CIF) called the NPCIFE (Non-Parametric Cumulative Incidence Function Estimator; Heisey & Patterson 2006). CIF is the sum of probabilities of death from a given cause C, times the probability of surviving previous time, eventually generating an increasing probability of dying from cause C, allowing for competing-risks. There is a keen interest in these methods, which are quite easy to implement and for a large panel of species (Griffin *et al.* 2011; Hurley *et al.* 2011; Mills *et al.* 2008; Obbard & Howe 2008; Sandercock *et al.* 2011; Sargeant *et al.* 2011; Webb *et al.* 2011). Hence, in this study the NPCIFE was used (Wild1 package) to generate accurate mortality risks and assess their relative importance within each predator community, and for each age class: fawns (animals in their first year), sub-adults (in their second year), prime-aged adults (2 – 6 yrs.), and senescent ( $\geq 7$  yrs.), as commonly categorized for roe deer (Gaillard *et al.* 1993b; Loison *et al.* 1999). These age classes are also suitable for the Grimsö roe deer population, according to the quadratic regression of the age-specific survival (Appendix 1).

♦ *Cox proportional hazards*

Unfortunately, there is no formal way of directly test differences between CIF's. Rather, Heisey and Patterson (2006) recommend the use of the Lunn & McNeil (1995) model, based on Cox Proportional Hazards. This is a very good complement to the CIF estimations, because the non-parametric form of Cox regressions does not necessarily require specifying a hazard function. For this method, the dataset is duplicated as many times as there are mortality causes. In this way, it prevents from over-parameterization of the model. I chose to stratify by mortality cause, because I aimed to get the hazard ratios of selected covariates for each mortality rates (survival package).

Covariates selection was done using the Akaike Information Criterion (AIC; Burnham & Anderson 2002). Before running the different candidate scenarios, correlation tests were performed to highlight possible colinearity between covariates (Appendix 2). In addition to those already mentioned ('Age class', 'Sex', 'Delayed', 'Migrant', and 'Snow'), the birth year of the individual ('Birth'), the consecutive years during which it was tracked ('Year') and the predator community ('Community' 1, 2, 3 or 4) were used for these correlation tests. Because the variables 'Year', 'Birth' and 'Community' were highly correlated ( $> 50\%$ ), only 'Community' was kept in the model selection because it was the most relevant to this study. The 'Birth' and 'Year' variables were originally set to encompass the inter-annual natural variation, but the redundancy was too high to keep them. Four variables ('Age class', 'Sex', 'Delayed' and 'Migrant') were used as a reference model. 'Age class' and 'Sex' were included because of their importance in the growth rate analysis (see Projection Matrix Model section). Further, they both had a significant impact on

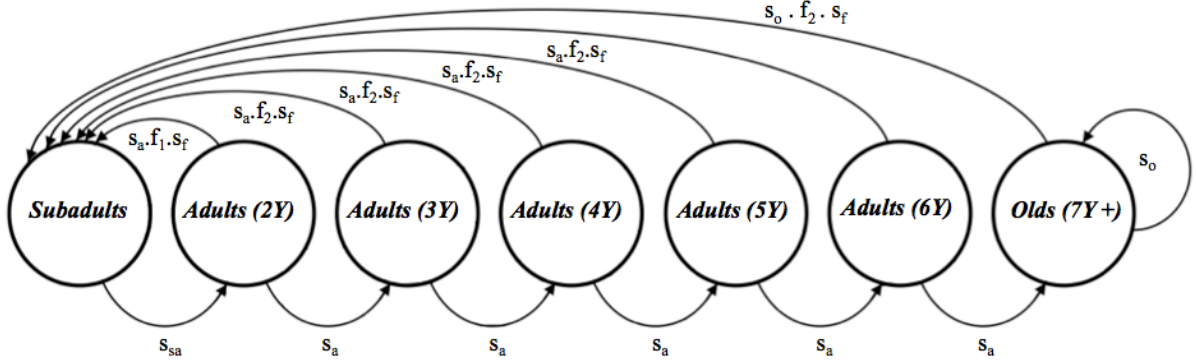
survival across strata (Age class: Hazard Ratio (HR) = 0.75, 95% C.I. = 0.65-0.86,  $z = -3.966$ ,  $P < 0.01$ ; Sex: HR = 0.80, 95% C.I. = 0.64-1.00,  $z = -1.973$ ,  $P = 0.048$ ) even if the ‘Age class’ variable did not satisfy the assumption of hazard proportionality ( $\rho = 0.19$ ,  $\chi^2 = 17.40$ ,  $P < 0.01$ ). This is due to the early decrease of fawns’ mortality (Fig. 1), as confirmed by looking at the Schoenfeld residuals. Results involving Age class should then be interpreted with caution. I also kept ‘Delayed’ and ‘Migrant’ because they correct for the animals that have been monitored less intensively.



**Figure 1.** Kaplan-Meier survival functions in four roe deer age classes: fawns (first year), subadults (second year), prime-aged adults (2 - 6 yrs.) and senescent ( $\geq 7$  yrs.). Fawns experienced an early decrease in survival, and prime-aged adults had the highest survival rates. For the sake of legibility, confidence intervals were not plotted. Data from Grimsö, South-central Sweden (1975-2012).

Cox regressions evaluate the hazard ratios between several levels of a given covariate. For instance, if the mortality risk is higher for males than for females, the hazard ratio is  $< 1.0$ , meaning that females have higher survival. If the hazard ratio of a categorical variable was proven significant, a detailed set of hazard ratios was obtained (script adapted from Heisey & Patterson 2006). For categorical variables like ‘Age class’, comparisons are made between each category and the reference category (Fawns-Subadults, Fawns-Adults, Fawns-Senescents). For ‘Sex’, the reference category is males, for ‘Age class’, it is fawns.

Hazard proportionality is the most important assumption behind these models (Murray 2006) and it was checked in the same way as previously, using the scaled Schoenfeld residuals (cox.zph function).



**Figure 2.** Pre-breeding diagram of the roe deer female population in GWRA. Prime-aged adults are split into 5 age classes that have the same probability of survival ( $s_a$ ); senescent animals (7Y +) is the absorbing class with constant survival ( $s_o$ );  $s_f$  and  $s_{sa}$  represent fawn and subadult survival respectively. Roe deer start reproducing in their second year (see also Gaillard *et al.*, 1992) with lower fecundity rate ( $f_1$ ) than the following years ( $f_2$ ). This diagram was used to parameterize four stochastic projection matrices, one for each risk regime related to predators' occurrence.

#### ♦ *Matrix Projection Model*

I used a 7-staged pre-breeding projection matrix to describe the roe deer population at GWRA (Fig. 2). The dataset allowed for estimation of the survival of senescent animals (seven years and onward, absorbing class) and therefore, prime-aged adults needed to be split into five age classes with equal survival. To parameterize the projection matrix, the survival estimates were extracted from standard Cox regressions (i.e. unduplicated dataset and using the covariates selected in the AIC analysis), with age classes as a factor. Reproductive rates were obtained from the ovulation rates of killed females. Then, I used Monte Carlo simulations (1,000 runs for each predator community), with estimates of survival and reproductive rates drawn from normal distributions. This stochastic approach provides good estimation and realistic distribution of growth rates ( $\lambda_1, \lambda_2, \lambda_3, \lambda_4$ ).

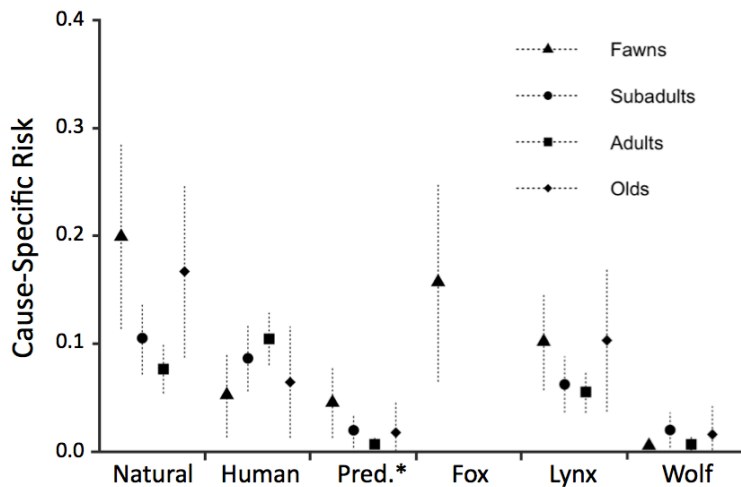
## RESULTS

Over the last 37 years, the total mortality risk was 31.1% (95% C.I. = 28.7-33.5), irrespective of age class, sex or snow condition. The risk of dying from natural, human or predation cause was quite even: 11.1% from natural and unknown causes (95% C.I. = 9.1-13.1), 8.7% from human-related causes (95% C.I. = 7.0-10.4) and 11.3% from predation (95% C.I. = 9.4-13.2). When segregating the predation into fox, lynx, wolf and residual predation, lynx appeared to be the one putting the roe deer at most risk (7.0%, 95% C.I. = 5.4-8.7) compared to fox (1.4%, 95% C.I. = 0.5-2.3) and wolf (1.1%, 95% C.I. = 0.4-1.7). Residual predation accounted for 1.7% (95% C.I. = 0.8-2.7).

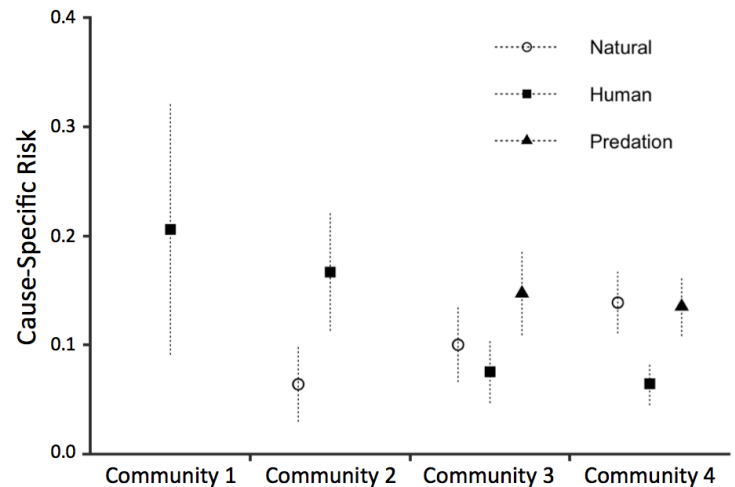
When stratifying the dataset by age class, fawns tended to have a much lower survival (Fig. 1). This was confirmed by the CIF: the sum of mortality risk was much higher for fawns (56%) than for subadults (29%) or prime-aged adults (25%); senescent animals had lower survival than the two intermediate age classes, with an annual mortality risk of (37%). This is consistent with the quadratic regression of age-specific survival (Appendix 1).

#### ♦ *Cumulative Incidence Function*

Among all risks, only human caused mortality tended to put more risk on the two intermediate age classes as natural mortalities and predation affect olds and fawns to a greater extent (Fig. 3). Fox, as expected, only preyed upon fawns, and the risk was equal to 15.7% (95% C.I. = 6.5-24.9). Wolf predation seems marginal, without any pattern of selection regarding roe deer age. CIF analyses stratified by age class also reveal a higher variance around fawns and senescent animals' estimates (Fig. 3).



**Figure 3.** Cause-specific risks calculated for each roe deer age class, using the NPCIFE (dotted lines represent the 95% confidence interval). All mortalities apart from human and wolf causes affect subadults and prime-aged adults to a lesser extent than fawns and senescent animals. Pred.\* stands for residual predation, i.e. eagle predation or unidentified predator. Data from 458 known age animals from Grimsö, South-central Sweden, 1975-2012.



**Figure 4.** Cause-specific risks in roe deer calculated in each community, using the NPCIFE (dotted lines represent the 95% confidence interval). Community 1 is the free-predator control; theoretically, Community 2, 3 and 4 consecutively add fox, lynx and wolf predation. Because of late summer fawns monitoring, no fox predation was documented before Community 3. Data from 458 known age animals from Grimsö, South-central Sweden, 1975-2012.

Human and natural mortalities displayed an opposite pattern, the former decreasing and the latter increasing with the number of predators (Fig. 4). Predation rates were quite even in the two most recent communities and forced total mortality to increase from 21% and 23% in Community 1 and 2 respectively, to 32% in Community 3 and 34% in Community 4. This trend is a strong support for an additive effect of predation on roe deer survival.

♦ *Cox regressions*

The four models included in the AIC selection were quite close to each other, and the one with the highest weight of evidence was kept (Tab. 1). As a result, the survival of roe deer was a function of the base covariates (Sex, Age class, Delayed and Migrant), Snow cover (expressed as the number of days above 30 cm of snow) and Community (based on occurrence of predators). The first part of the analysis consisted in Cox regressions with a set of three risks: Natural, Human and Predation (Tab. 2). In accordance with CIF analysis, Natural and Predation hazards were significantly higher for fawns compared to subadults and prime-aged adults; however Age Class did not satisfy the hazard proportionality assumption in the Predation stratum ( $\rho = 0.41$ ,  $\chi^2 = 47.3$ ,  $P < 0.01$ ). Fawns did not have higher survival regarding Human risks, presumably because of their susceptibility to hay-mowing and traffic accidents. Sex played a minor role in the regressions: it neither affected Natural nor Predation risks, and even if the hazard ratio was in favor of females in Human-related causes (HR = 0.38, 95% C.I. = 0.24-0.64,  $z = -3.72$ ,  $P < 0.01$ ), hazards were not proportional ( $\rho = 0.23$ ,  $\chi^2 = 6.29$ ,  $P = 0.01$ ) because of the hunting seasonality — happening mostly in August. Snow had an obvious impact on Natural and Predation risks, decreasing survival by 0.5% for each additional day with more than 30 cm. Results regarding Community effect are consistent with the CIF analysis, confirming the increase in Natural mortality and the decrease in Human-related causes, with more predator species. No significance was detected between Community 3 and 4 regarding Predation risks (HR = 0.62, 95% C.I. = 0.32-1.02,  $z = -1.87$ ,  $P = 0.06$ ), meaning that predation risk was stable. All these results were similar using the alternative dataset and autopsy accuracy, i.e. alternative death cause in unclear cases, is not discussed further for this first analysis.

**Table 1.** Model selection using Akaike Information Criteria showing the number of parameters (K), difference between model AIC and best-ranked model ( $\Delta AIC$ ) and Weight of evidence ( $w$ ). The reference model (RM) includes Sex, Age class, Delayed status, and Migratory status.

Model Rank	Model	K	$\Delta AIC$	$w$
1	(RM) + Snow + Community	6	0	0.548
2	(RM) + Community	5	1.5	0.262
3	(RM) + Snow	5	2.9	0.127
4	Reference Model (RM)	4	4.4	0.062

**Table 2.** Hazard ratios from Cox regressions using Lunn & McNeil method (1995), for each roe deer mortality risk (Predation risks pooled together in the first table, split in the second) with associated p-value and 95% confidence interval. A hazard ratio > 1.0 corresponds to a decrease in survival for each additional unit of the covariate. When a categorical variable was significant for a given risk (Age class or Community), a comparison between the different levels was performed (see Heisey & Patterson 2006); numbers in parentheses show what levels were compared. Data from 458 known age animals from Grimsö, South-central Sweden, 1975-2012.

Covariate	Natural			Human			Predation		
	Hazard ratio	p-value	95% C.I.	Hazard ratio	p-value	95% C.I.	Hazard ratio	p-value	95% C.I.
<b>Age class</b>	<b>0.69</b>	<b>&lt; 0.01</b>	<b>[0.54-0.90]</b>	<b>1.38</b>	<b>0.04</b>	<b>[1.02-1.88]</b>	<b>0.64 †</b>	<b>&lt; 0.01</b>	<b>[0.51-0.82]</b>
	0.48 (1-2)	< 0.01	[0.28-0.82]	1.57 (1-2) †	0.33	[0.63-3.91]	0.46 (1-2) †	< 0.01	[0.27-0.78]
	0.35 (1-3)	< 0.01	[0.21-0.59]	2.16 (1-3)	0.07	[0.93-5.02]	0.32 (1-3) †	< 0.01	[0.20-0.53]
	0.66 (1-4)	0.32	[0.30-1.49]	2.43 (1-4)	0.18	[0.66-8.96]	0.60 (1-4) †	0.13	[0.31-1.16]
<b>Sex</b>	1.09	0.69	[0.73-1.62]	0.39 †	< 0.01	[0.24-0.64]	1.06	0.75	[0.73-1.54]
<b>Snow</b>	1.005	0.04	[1.00-1.01]	0.99	0.08	[0.99-1.00]	1.005 †	0.04	[1.00-1.01]
<b>Community</b>	<b>1.61</b>	<b>&lt; 0.01</b>	<b>[1.22-2.14]</b>	<b>0.59</b>	<b>&lt; 0.01</b>	<b>[0.48-0.73]</b>	0.62 (3-4)	0.06	[0.38-1.02]
	2.28 (2-3)	0.04	[1.04-5.01]	0.76 (1-2)	0.39	[0.41-1.42]			
	2.70 (2-4)	< 0.01	[1.30-5.58]	0.27 (1-3)	< 0.01	[0.14-0.54]			
				0.24 (1-4)	< 0.01	[0.13-0.44]			

Covariate	Fox			Lynx			Wolf		
	Hazard ratio	p-value	95% C.I.	Hazard ratio	p-value	95% C.I.	Hazard ratio	p-value	95% C.I.
<b>Age class</b>	-	-	-	0.83 †	0.20	[0.63-1.10]	0.88	0.65	[0.51-1.51]
<b>Sex</b>	0.48	0.21	[0.15-1.51]	0.93	0.76	[0.59-1.48]	1.31	0.65	[0.40-4.26]
<b>Snow</b>	0.99	0.21	[0.98-1.01]	1.00	0.46	[1.00-1.01]	1.02	< 0.01	[1.01-1.04]
<b>Community</b>	1.26	0.34	[0.78-2.05]	0.70	0.24	[0.39-1.27]	-	-	-

Age class: 1=Fawns; 2=Subadults; 3=Prime-age adults; 4=Senescent adults

Sex: reference is Males (1=Males; 2=Females)

† : issues regarding proportionality of hazards ( $P < 0.05$ )

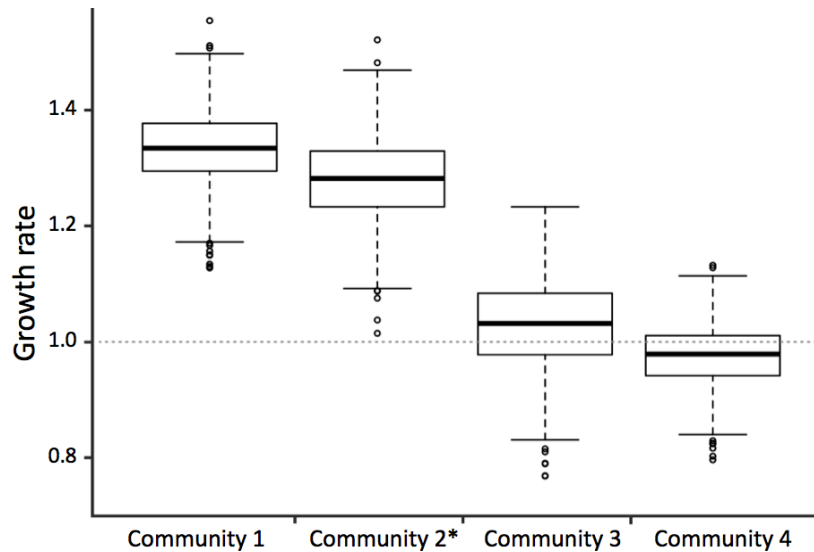
Predation was then split to quantify the effect of each covariate for each predator species (Tab. 2). Residual predation results were meaningless because hazard proportionality assumptions were not met for the following covariates: Age class ( $\rho = 0.58$ ,  $\chi^2 = 16.77$ ,  $P < 0.01$ ), Snow ( $\rho = 0.52$ ,  $\chi^2 = 10.08$ ,  $P < 0.01$ ) and Community ( $\rho = 0.53$ ,  $\chi^2 = 7.51$ ,  $P < 0.01$ ), and the fox, lynx and wolf strata respectively failed to unravel sex biased selection patterns (Tab. 2). Further, no effect of prey selection among age classes in lynx or wolf was significant either (Tab. 2). Snow only affected wolf predation (HR = 1.02, 95% C.I. = 1.01-1.04,  $z = 3.129$ ,  $P < 0.01$ ), the assumption of proportional hazard being met ( $\rho = -0.24$ ,  $\chi^2 = 1.30$ ,  $P = 0.25$ ) and there is a sharp effect on survival, which decreases by 2% for each additional day of more than 30 cm of snow. Finally, Community did not affect fox and lynx predation, meaning that wolf predation may be additive. Though, the effect of wolf predation is quite low, and that is why predation risks do not increase that much between Community 3 and 4 (Tab. 2).

♦ *Population growth rates*

To evaluate how the gradually recovering predator community affects roe deer population growth ( $\lambda$ ), I defined the projection matrix for each community (Fig. 4). I used estimates from Community 2 as a control, since only Human-related and Natural mortalities were detected. To obtain a population growth estimate for a population under the fox predation risk, I inferred decreased fawn survival by 14%, an estimate published from the same study area (Nordström 2010) and kept other rates constant; this would avoid additional bias, assuming no impact of fox predation on human and natural mortalities. Genuine values from Cox regressions were used to parameterize Community 3 and Community 4 projection matrices (Tab. 3). Two reproductive rates were applied to subadult ( $\mu_1 = 1.757$ , Standard Error (S.E.) = 0.098) and adults females ( $\mu_2 = 2.271$ , S.E. = 0.044). When generating the projection matrix, reproductive rates were multiplied by 0.9 (approximately 10% of unfertilized eggs) and by 0.5 (assuming even sex ratio).

**Table 3.** Survival rates (and standard errors) of each roe deer age class obtained from the Cox regressions for each community. Here, Community 1 is actually the Community 2 in the survival analysis, and Community 2\* is the same as Community 1 plus a risk of predation from fox (14%, see Nordström, 2010). Data from 233 known age females from Grimsö, South-central Sweden, 1975-2012.

	Fawns		Subadults		Prime-aged Adults		Olds	
	Survival	Standard error	Survival	Standard error	Survival	Standard error	Survival	Standard error
Community 1	0.93	0.0538	0.836	0.0870	0.885	0.0494	0.790	0.214
Community 2*	0.79	0.10	0.836	0.0870	0.885	0.0494	0.790	0.214
Community 3	0.332	0.108	0.691	0.0839	0.884	0.0387	0.770	0.0944
Community 4	0.544	0.0763	0.703	0.0550	0.738	0.0377	0.559	0.1147



**Figure 5.** Roe deer population stochastic growth rate distributions for each community (1.000 simulations each). Dotted line corresponds to a stable population growth rate ( $\lambda = 1.0$ ). Data from 233 known age females from Grimsö, South-central Sweden, 1975-2012.

Roe deer population growth rate decreased in Community 2 when adding fox predation alone, but the largest impact was when the lynx was re-established (Fig. 5). Indeed, lynx presence lowered the growth rate by 17% in Community 3. As previously mentioned, wolf predation seems to be additive and the combination of the three predators brought the population growth rate under the  $\lambda = 1.0$  threshold. This trend in population growth rate is mainly driven by juvenile rates, and secondly by lower survival of adult females (prime-aged and old animals), as suggested by the survival values.

## DISCUSSION

The long-term monitoring of this study suggests that re-colonizing predators play an important role in regulating roe deer population dynamics. In summary (i) predation mortality was largely additive to the pre-existing risk set (natural and human-related mortalities); (ii) compensation and additive patterns between predation risks could not be determined with certainty, but additivity should prevail; (iii) roe deer age classes and genders were differently affected by the several competing risks, even if no clear evidence was found for predation in Cox regressions; (iv) population growth rate decreased with increasing number of predator species, down to levels that may explain the recent roe deer decline in GWRA.

### ADDITIVE EFFECT OF PREDATION

Predation risks were largely additive to natural and human-related mortality causes, increasing total mortality risk by approximately 40% as expected in prediction (2). This large increase is attributable to the different patterns of predation displayed by the fox, the lynx and the wolf: all roe deer age classes irrespective of sex were affected by predation and that is why the effect is so strong. Additivity of predation risks has been assessed in a wide range of ungulate species worldwide, and its magnitude depends on the context. For instance, elk calves (*Cervus elaphus*) experienced increased mortality risks under severe environmental conditions in Yellowstone National Park (Singer *et al.* 1997); in the Kruger National Park, South Africa, the additive effect of predation was the best explanation of roan antelope (*Hippotragus equinus*) decline (McLoughlin & Owen-Smith 2003), and moose (*Alces alces*) were proven to endure additive predation from wolves (*Canis lupus*) and bears (*Ursus arctos* and *Ursus americanus*) at low population densities (Gasaway *et al.* 1992). In their review, Melis *et al.* (2009) emphasize the importance of environmental productivity and winter harshness regarding predation effects. Scandinavia is therefore a unique place in Europe since the winter can be very tough, implying greater predation impacts on roe deer survival. The winter harshness seems to affect natural and predation risks in GWRA, especially when considering wolf predation. A possible explanation could be that roe deer escape less easily when snow depth increases, consequently simplifying for the wolf (who is not a roe deer specialist) to track and eventually catch it. Alternatively, wolf predation could act slightly compensatory to natural mortality causes like starvation, and become more successful in killing emaciated roe deer as winter

severity increases. Unexpectedly, the hazard ratio for lynx was equal to 1.0, meaning that winter severity did not influence lynx predation on roe deer, even though climatic factors have been shown to alter lynx predation in South-eastern Norway (Nilsen *et al.* 2009).

The Cumulative Incidence Function is also a tool to describe temporal trends in competing risks. The decline of human-related mortalities is closely linked to the change in hunting regulations in GWRA (hunting corresponded to 80.2% of human-related mortalities). At the beginning of the study roe deer were deliberately killed in order to retrieve the collars and this explains the high mortality in Community 1 and partly in Community 2. Then, human-related mortalities gradually decrease, and the hunting effort is much lower than in an ordinary hunting ground (Fig. 3). Over the last 40 years, hunting activity was maintained at low levels, taking a maximum of 90 individuals per year. The proportion of ‘natural mortality causes’ increases with increasing predator complexity. First, this suggests that the timing of retrieved deaths is a critical component of competing-risks analyses. An autopsy at the kill site can be very difficult when it comes to distinguish between predation and scavenging. The most difficult case is if the collar is found alone on the ground and the only mortality case that can be ruled out is intentional and legal hunting. Neither evidence nor signs of roe deer poaching have ever been found at the GWRA. Therefore it is fair to assume that when only a collar is retrieved, it stems from an event of ‘natural’ mortality. The recent use of GPS technology and its implementation in GWRA will hopefully shorten the time between the mortality event and the autopsy, and thus improving the possibility to identify the death cause (see also Zens & Peart 2003). It will also improve the determination of the true killing site, since it is not unusual that the predator or scavengers (red fox) move the carcass or the collar. Alternatively, an explanation for this increasing proportion of ‘natural mortality causes’ could be the ‘super-additive’ nature of predation risks, as suggested by Sandercock *et al.* (2011). This happens when the addition of a given risk strengthen another risk at the same time, which could be the case to a certain extent in GWRA. An analysis with the less conservative dataset (see Methods) showed that natural mortalities were a bit lower in Community 3 (9.3% against 10%) and tended to level off in Community 4 (10.9% against 13.9%), but this was not sufficient to rule out the super-additive hypothesis.

#### FOX, LYNX AND WOLF RISKS

After natural mortality, fox was the greatest risk for fawns in GWRA (15.7%, CIF) and comparable to a similar area in northern Norway (13%); in the same study, Panzacchi *et al.* (2008) found that this rate increased for roe deer living in more open habitats with a higher population density (25%), a pattern confirmed in other areas within Sweden (40% in southern Sweden, see Jarnemo *et al.* 2004) or outside Sweden (48% on an Norwegian island, see Aanes & Andersen 1996). Unfortunately, in GWRA, fox predation has not been documented without the presence of lynx because tracking of summer fawns began in 2000 in Grimsö (Fig. 4). Indeed, the first collared roe deer killed by a predator was reported in 1997

(lynx kill) and first confirmed fox kill was documented in 2001. However, the four communities were kept in the models for three reasons; first, because they were a good surrogate of time variables (thereby including inter-annual variations, see Methods), second, because during the two periods of fox being the only predator (between 1976 and 1982, and later between 1990 and 1996), fawns were still at risk in the wild even if we cannot detect it in the analysis; and third, because natural as well as human mortality causes evolved between Community 1 and Community 2 (Fig. 4).

However, having noticed that fox mortality affected only fawns, total predation rates in Community 2 is expected to be much smaller than the ones found in Community 3 and 4, thereby partially validating prediction (3). The low fox predation rate in GWRA makes them available for sympatric predators as was the case of lynx and wolf that both preyed upon all age classes, thereby suggesting that together they have an important additive effect on also subadult and adult survival rates.

One might question the contradictory results between the Cox regressions analysis and the CIF's. Indeed, the NPCIFE showed that predation remained constant between Community 3 and 4, implying that by adding wolf predation, the system compensates for the other risks. However, according to the second set of analysis (predation specific), was the Community effect not significant for fox, lynx and 'unknown' predation hazard ratios (see Tab. 2), suggesting that the addition of wolf predation to the system was not followed by a significant change in other predation rates and consequently it could be interpreted as wolf mortality being additive. First, the two analyses are not completely comparable as the Cox regressions contain several explanatory variables such as Sex, Snow index, Migratory status etc. that the CIF's are lacking. Second, wolf predation is still very low (2,1%, CIF), because roe deer only plays a secondary role in the wolf diet when moose are available in the area (Mattioli et al. 2004), as in the GWRA. Nevertheless, wolf may become an increasingly important factor in the coming years because of an observed switch in predation activity in recent years (Kjellander & Andrén unpubl.). When the first "Uttersberg-pack" was established, the territory only overlapped with approximately one third of the GWRA (Viltskadecenter, online annual publications) and according to unpublished data on kill rates (Sand *et al.* unpubl.) from that pack the predation rate was very low, and the wolves rather fed on road and railroad kills. Today, the new "Hedbyn-pack" has established and their territory overlap completely with the entire GWRA and they actively preyed upon both roe deer and moose (Sand *et al.* unpubl.). Out of that, it is hazardous to draw any conclusions in terms of competition between the four predators. If we stick to the more detailed Cox regressions, wolf could be an additive source of mortality for roe deer. No pertinent information could be obtained from 'unknown' predation mortalities, because of hazard proportionality issues (global fit:  $\chi^2 = 22.70$ ,  $P < 0.01$ ). However, they totally disappeared when using the model with 'alternative causes' (global fit:  $\chi^2 = 10.35$ ,  $P = 0.07$ ) and roe deer survival was 8 times lower in Community 4 than in Community 3 (HR = 8.5, 95% C.I. = 1.07-67.3,  $z = 2.031$ ,  $P = 0.04$ ). This pinpoints the importance of improving the methods to detect mortality causes. Because they concern a non-negligible number of death

events ( $n = 21$ ), it would be of prime interest to know if they are spread among all predators, or if they are attributed to a single species, to strengthen the conclusions about additive vs. compensatory mortality.

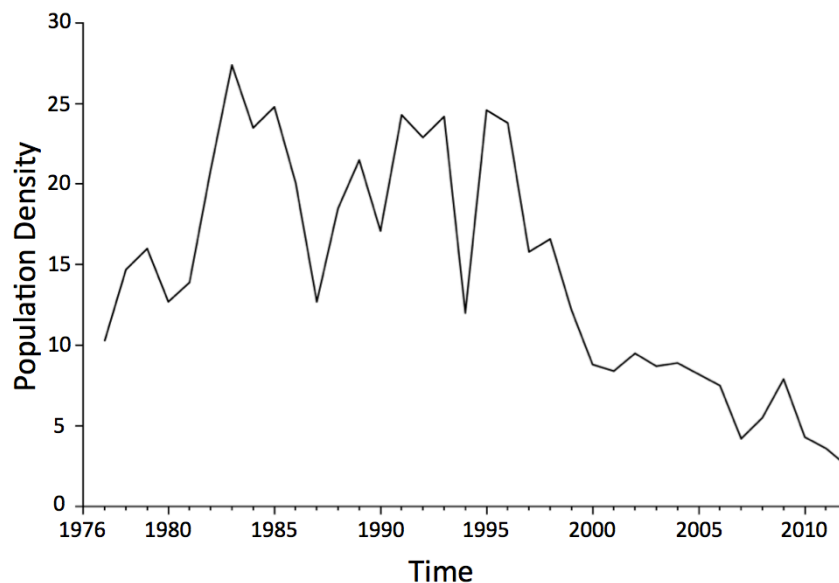
A further step would be to include predator density in the models in order to improve the accuracy of roe deer survival estimates. For instance, roe deer survival tended to be less affected by lynx predation in Community 4 than in Community 3 ( $HR = 0.70$ , 95% C.I. = 0.39-1.27) even if this change was not significant ( $z = -1.173$ ,  $P = 0.24$ ). This could be explained by a recent decrease in lynx density in GWRA, which could potentially allow wolf to take over and would support either the compensatory or additive nature of lynx and wolf predation. Moreover, because climatic variations may drive different responses in predator behaviour (Post *et al.* 1999), the interaction between weather and predation risks could potentially reveal the interplay of these two factors and their effect on roe deer survival (Griffin *et al.* 2011; Hebblewhite 2005).

## ROE DEER POPULATION GROWTH RATE

In their review of neonatal mortality of ungulates, Linnell *et al.* (1995) claim that “*despite the prominent role of predation, little is known about its long-term compensatory or additive nature, and therefore its impact on population dynamics is unclear*”. Besides, studies of ungulate survival is often restricted to one age class (Gaillard *et al.* 1997; Griffin *et al.* 2011; Gustine *et al.* 2006; Singer *et al.* 1997), one sex (Ballard *et al.* 2000; Delgiudice *et al.* 2002; Kjellander *et al.* 2004), or within a limited time-frame (Aanes & Andersen 1996; Panzacchi *et al.* 2008). To my knowledge, roe deer survival has never been studied under a competing-risk framework, notably risks related to sympatric predators. Since roe deer is one of the most common large herbivores in Europe, thus prone to a large panel of predators (Melis *et al.* 2009), there was a great need to fill the information gap.

In this context, the data accumulated in GWRA provides a good insight on roe deer population dynamics because the survival analysis gives estimates for each age class with varying environmental conditions. The general pattern of age-specific-survival in GWRA followed a U-shaped relationship (Appendix 1), as commonly found in the literature (Delgiudice *et al.* 2006). Using the same method as Loison *et al.* (1999), i.e. re-scaling the origin of the quadratic form of age to 7 years old, females had higher survival than males ( $\alpha_F = 0.85 \pm 0.05$  against  $\alpha_M = 0.64 \pm 0.04$ ), survival decrease was less important ( $\beta_F = -0.03 \pm 9.0e^{-3}$  against  $\beta_M = -0.11 \pm 0.02$ ) and the acceleration of senescence was lower ( $\gamma_F = -0.01 \pm 2.7e^{-3}$  against  $\gamma_M = -0.02 \pm 4.3e^{-3}$ ), confirming prediction (1). Such differences were already detected at age 6 and the cutting point in senescence is probably between 6 and 7 years of age. This pattern of senescence should mainly be explained by the physiological nature of aging and to a lesser extent by predation as such. The CIF plots suggest that lynx predation might be slightly selective by nature even if not significant ( $P = 0.20$ ) and the most probable predator capable of shaping this trend.

Juvenile survival is an important determinant in ungulate population trajectories (Gaillard *et al.* 2000) and fox together with lynx play a major role in reducing fawn survival (Tab. 3). From that, high and constant survival rates of adult females are necessary for maintaining population growth rate. Not only were fawns affected by predation rates from Community 1 to Community 4 but also the reproducing classes, due to the addition of lynx and wolf predation (prediction 4). The impact of lynx predation was the most striking, which is in accordance with Gervasi conclusions (Gervasi *et al.* 2011). They claim that lynx should play a relatively greater role than red fox predation at low roe deer densities, like in GWRA. As a result, population growth rate dropped with an increasing number of predators and flattened in Community 4. However, it is quite early to reject prediction (5) because the additive nature of wolf predation may increase in the future, as previously discussed. Because  $\lambda_4$  was inferior to 1.0, the future of the roe deer population in GWRA is uncertain and should currently be considered as a sink population dependent on immigration to sustain (Pulliam 1988). The combined predation of fox, lynx and wolf is therefore likely to be responsible for the progressive decrease of roe deer density over the last 15 years (Fig. 6), given that human harvest has been decreasing and kept at low levels over this time period (6.4% human-related mortality risk in Community 4; 95% C.I. = 4.5-8.4).



**Figure 6.** Roe deer population density over the last 36 years, based on annual pellet counts (percentage of plots with roe deer faeces, after Pehrson 1997). Density has decreased sharply since 1996. Data from Grimsö, South-central Sweden, 1976-2012.

Out of all that, what can we expect for the roe deer future in central Sweden? Two alternatives may arise; first, roe deer life-history cycle may slow down for a while, as a result of harsh conditions: Nilsen *et al.* (2009) highlighted a negative correlation between population growth rate and generation time and called it a “roe deer hell” for declining populations like in GWRA. Second, by lowering population density, reproductive success might be improved resulting in a ‘healthier’ population. This could be

mediated by body weight, which is density-dependent (Toïgo *et al.* 2006) and proven to positively influence reproductive success (Gaillard *et al.* 2000). Then, if roe deer densities reach a critical value, the viability of the population may be questioned, but this is improbable for a species with such a high reproductive potential.

## RECOMMENDATIONS FOR THE FUTURE

The decline in roe deer densities is clear enough to question the sustainability of hunting activities in GWRA. If we are to stop the population decline, the easiest mortality cause to manipulate is human harvest through hunting regulations. However, its relative importance on roe deer survival has obviously changed over time, and the results show that nowadays, re-colonizing predators bring an additional mortality risk at least twice as big as the one from human-related mortality causes. Therefore, from a survival viewpoint, banning hunting in GWRA would have a limited impact on population growth rate both because of its secondary importance, and because human harvest takes very few juveniles that were proven to be the principal driver of population growth rate trajectory. Nevertheless, higher hunting rates would for sure not be sustained by roe deer population. On the other hand, human harvest targeting mainly adult males, animals that are omitted in the projection matrix models although they are still involved in the reproductive success, it is possible that the population decline also owes to intrinsic properties of the male population. A deeper investigation of fecundity and reproductive success would perhaps give more support for the potential impact of hunting on the male population and lead to safer decisions regarding hunting regulations.

Secondly, because predation has become a key factor of roe deer survival in GWRA, the issue regarding redundancy between predation and unknown causes need to be solved, in order to efficiently test the superadditive hypothesis of predation. In the case of GWRA, superadditivity of mortality (or ‘depensation’) could happen because of predator saturation, environmental conditions or a combination of both (Liermann & Hilborn 2001). Because depensation effects are poorly described for low-density populations, this test would be particularly relevant in GWRA where roe deer density is indeed very low. If confirmed, the effect on roe deer dynamics could be disastrous and would require thorough management of the population in South-central Sweden.

Finally, to investigate the driving forces behind competing mortalities, I used Lunn & McNeil (1995) method applied to Cox Proportional Hazards because it was the most relevant model. However, Cox regressions require continuous hazards through time, which forced me to assume continuous survival when animals were lost for tracking for a given time interval. Andersen-Gill models (1982), a counting-process analogue to the Cox Proportional Hazards could be a way to account for complex monitoring

patterns with gaps and discontinuous hazards (Murray 2006), but examples of studies using this model in a competing-risk framework were scarce (Delgiudice *et al.* 2002).

Hazard proportionality issues raised by age classes in the models could be removed by an analysis of seasonality in the competing risks (using the ‘muhaaz’ package). Finally, this dataset accumulated through the last 40 years by the Grimsö Wildlife Research personal could be perfectly suitable for a Bayesian approach, computationally demanding but statistically very strong and informative.

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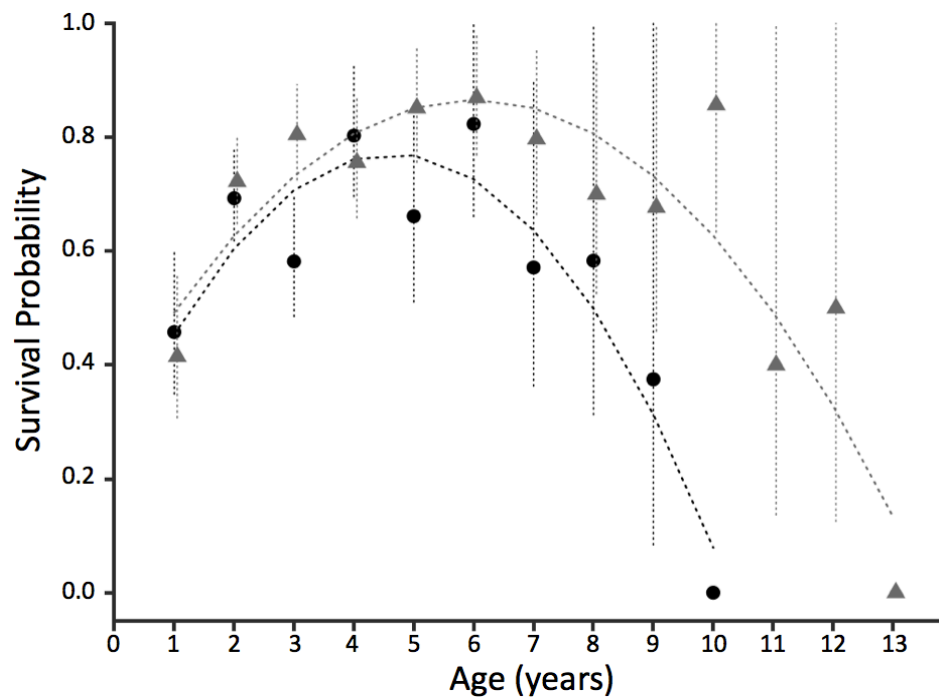
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## **APPENDICES**



**Appendix 1.** Age-specific survival of male (circles,  $n = 225$ ) and female (triangles,  $n = 233$ ) roe deer; vertical dotted lines represent the 95% confidence interval around the annual estimates. Non-linear regression lines were obtained with age in a quadratic form. Data from known age animals from Grimsö, South-central Sweden, 1975-2012.

**Appendix 2.** Correlation tests performed between the potential candidates of covariates for the Cox Proportional Hazards. Level of acceptance was set to 0.5; numbers' font in the lower panel is proportional to the level of correlation. Data from 458 known age animals from Grimsö, South-central Sweden, 1975-2012, and from Ställdalen meteorological station (39km North-West from GWRA, Swedish Meteorological Institute, SMHI).

From top left to bottom right: Birth (birth year of the roe deer), Sex, Migrant2 (migratory status: stationary, disperser or migrant), Delayed (animals that entered the study at least one year after their first capture), Year, Age, Age class, Snow, Community.

