The decline of a mesopredator

Is it caused by the return of apex predators?

Emelie Sabrie

Degree project in Biology • 30 credits • Master's thesis
Swedish University of Agricultural Sciences, SLU
Faculty of Forest Sciences • Department of Ecology
Uppsala 2025

The decline of a mesopredator: Is it caused by the return of apex predators?

Minskningen av en mesopredator: Är det på grund av återkomsten av stora rovdjur?

Emelie Sabrie

Supervisor:	**Camilla Wikenros, Swedish University of Agricultural Sciences, Department of Ecology**
Assistant supervisor:	Henrik Andrén, Swedish University of Agricultural Sciences, Department of Ecology
Examiner:	Håkan Sand, Swedish University of Agricultural Sciences, Department of Ecology

Credits: 30 credits
Level: Master's level (A2E)
Course title: Master's thesis in Biology, A2E – Faculty of Forest Sciences
Course code: EX1040
Course coordinating dept: Department of Wildlife, Fish, and Environmental Studies

Place of publication: Uppsala
Year of publication: 2025

Keywords: Eurasian lynx, intraguild predation, red fox, wolf

Swedish University of Agricultural Sciences
Faculty of Forest Sciences
Department of Ecology
SLU Grimsö Wildlife Research Station

Abstract

The relative strength of top-down and bottom-up trophic control vary depending on abiotic and biotic conditions. Predators occupying the highest level, such as wolf (*Canis lupis*) and lynx (*Lynx lynx*), have the potential to exert a negative impact mesopredators, such as the red fox (*Vulpes Vulpes*). This study investigates the population development of the fox population at Grimsö Wildlife Research Area in south central Sweden. The analysis was based on a dataset that spans over 50 years including top-down (wolf, lynx and sarcoptic mange), and bottom-up variables (voles (*Clethrionomys glareolus* and *Microtus agrestics)*, roe deer (*Capreolus capreolus*) and hares (*Lepus europaeus* and *Lepus timidus*)) which have previously been identified to have a significant effect on the population dynamics of the fox. The temporal scope of this dataset includes the time prior to, during and post-reestablishment of wolves and lynx. The presence of sarcoptic mange and wolves had a significant and negative effect on the fox population. A similar result was not found for lynx. Nonetheless, lynx had already established in the area before wolves, which coincided with a decline in the fox population. This indicates that the presence of both apex predators has led to a negative cumulative effect on the fox population. In addition, it was demonstrated that voles continue to be of positive significance for foxes as this relationship remain strong in the absence and presence of apex predators and sarcoptic mange, however with a marked decrease. It is evident that the fox population is limited by both top-down and bottom up forces. This study is of importance in the context of biodiversity as the return of apex predators may result in cascading effects that benefit lower trophic levels and contribute to greater biodiversity.

Keywords: Eurasian lynx, intraguild predation, red fox, wolf

Table of contents

List of tables

List of figures

1. Introduction

An ecosystem can be regulated in a bottom-up or a top-down manner (Fretwall & Barach, 1977). These effects may also occur concomitantly within the same system (Elmhagen & Rushton, 2007; Hunter & Price, 1992). In predator-prey models such as Lotka-Volterra, both factors are a fundamental prerequisite. Moreover, the significance of these effects can switch in the aftermath of an event such as an epizootic (Wilmers et al., 2006) or due to significant changes at the top level e.g. presence/absence or high/low densities of apex predators (Elmhagen et al., 2010). Due to the dynamics inherent within food webs, changes are often imperceptible, and the effects may have a temporal lag (Estes et al., 2011). It is common that changes are only discernible after the species in question are gone extinct (Estes et al., 2011).

Bottom-up regulation is principally derived from the production level, where resource elements act as the limiting component in the system and determine the structure of food webs (Fretwall & Barach, 1977). The interactions among species, i.e. competition, may influence biomass and the complexity of food webs (Power, 1992). According to ratio dependent models, there will be concomitant increase of biomass at all levels when productivity levels are rising (Mittelbach et al., 1988; Terborgh et al., 1999). This is in contrast to prey dependent models, in which a system that is regulated in a top-down manner, the odd levels will thrive, and the ones below will be regulated by the consumers above them in the hierarchy (Fretwell & Barach, 1977; Oksanen et al., 1981; Oksanen & Oksanen, 2000; Terborgh et al., 1999).

Red foxes (*Vulpes vulpes*, hereafter fox) are known to be affected by both top-down and bottom-up processes (Elmhagen & Rushton, 2007; Elmhagen et al., 2010). They are among the most widespread species of mammals worldwide (Lariviere & Pasitschniak-Arts, 1996). Presumably, this is due to the fact that they are generalists both in terms of their dietary (Lindström, 1982) and habitat preferences (Weber & Meia, 1996). Their presence has been documented in various geographical locations, ranging from alpine regions to arable land and urban areas with high population density showing a profound ability to acclimatize to a multitude of environments (Englund, 1980; Scholz et al., 2020; Walton et al., 2017). Their ubiquity aligns with their status in Sweden, as they are found throughout the country and are classified as "least concern" according to the Red List (SLU Artdatabanken, n.d.).

The primary food source of fox are voles (*Clethrionomys glareolus* and *Microtus agrestis*), moreover, they also consume roe deer fawns (*Capreolus capreolus*), hares (*Lepus europaeus* and *Lepus timidus)*, and grouse (*Lyrurus tetrix* and *Tetrao urogallus*) as secondary food sources (Angelstam et al., 1985; Cederlund & Lindström, 1983; Lindström, 1982; Lindström et al., 1994; Kjellander & Nordström, 2003). Fox numbers follow the 3–4-year cycle of voles, which alternate between low and high numbers, and they switch to their alternative prey species during the voles' low phase number (Angelstam et al., 1985; Kjellander & Nordström, 2003; Lindström, 1983). In the northern parts of Sweden this relationship is stronger while in the southern parts fox populations tend to be more stable and density dependent (Lindström, 1994). In addition, their diet also consists of carcasses of inter alia herbivorous animals that have been killed by other predators, such as wolf (*Canis lupus*) and Eurasian lynx (*Lynx lynx*), or that have perished due to natural causes (Jędrzejewski et al., 1989; Helldin et al., 2007; Wikenros et al., 2013).

The return of the wolf has provided species, including but not limited to foxes, with a continuous influx of food in the form of moose (*Alces alces*) and roe deer carcasses. Consequently, this has led to a more evenly spread of food availability, as opposed to previously when there was only one peak during the hunting season (Wikenros et al., 2013). This is a vital resource that benefits foxes predominantly during the spring. Research has revealed that foxes exhibit elevated rates of carcass consumption around April and May, indicating that it serves as a significant component in their diet during a pivotal phase of their life cycles as parturition coincides with the spring season (Wikenros et al., 2014), in which their dietary needs increases approximately by two-fold (Lindström 1988).

For decades, predictions have been made that apex predators, such as the wolf and lynx, have a negative effect on foxes and in the event of their return to former areas, the ecological dynamics of foxes would be altered (Cavallini, 1996;

Lindström et al., 1994). In accordance with trophic cascade theory, if alterations in the fox population size appear due to variation in the absence or presence of apex predators, conclusions can be drawn that top predators are likely to have a strong influence on the fox population (MacArthur, 1972; Paine, 1980). This was evident in Sweden where it was demonstrated that after wolf and lynx declined, fox numbers increased, which aligns with the mesopredator release hypothesis (Elmhagen & Rushton, 2007). Albeit, the strength and significance of the top-down effect was influenced by the productivity of the ecosystem. In productive regions, it was proven to be controlled in a top-down manner, i.e. the increase in population size of foxes was associated with the decline of the two apex predators. In contrast, in the less productive regions in the northern parts, the fox population was instead controlled bottom up (Elmhagen & Rushton, 2007).

The nature of the interaction between lynx and wolf with foxes is best classified as intraguild predation, as the aforementioned species kills and prey upon on the latter (Palomares & Caro 1999). Notably, in most observed cases they are not consumed (Sunde et al., 1999). Intraguild predation predominantly occurs in instances where predators are similar in terms of body mass (Palomares & Caro 1999). Basically, there is a lower limit in terms of body size, meaning that the smaller predator should be of adequate size to be viewed as a successful competitor, thereby reducing the apex predator's access to key resources (Donadio & Buskirk 2006). Conversely, a similar upper limit also exists, stipulating that the smaller predator should not exceed a certain size due to the increased risk of mortality for the apex predator in case of confrontation.

The mesopredor release hypothesis predicts that the absence of apex predators within an ecosystem gives rise to a series of ecological consequences (Soulé et al., 1988). Specifically, it is predicted that their absence leads to numerical release for mesopredators, which in turn are able to increase in abundance and distribution. Therefore, under the absence of apex predators mesopredators are capable of exerting a greater level of predation pressure on their prey (Lindström et al., 1994; Soulé et al., 1988; Sovada et al., 1995). Extensive research has been conducted on the subject, yielding a range of outcomes (reviewed in Jachowski et al., 2020). Such findings indicate that mesopredators may exhibit divergent responses in disparate systems (van Schaik et al., 2025). Another hypothesis related to mesopredators and apex predators is the enemy constraint hypothesis which posits that top-down control peaks at the core of the apex predator ranges as the density tends to be highest in those areas (Newsome et al., 2017).

Winter conditions have been proven to have a negative impact on foxes as well as their prey (Andrén & Liberg, 2015; Bartoń & Zalewski, 2007; Kjellander & Nordström, 2003; Lindström, 1983; Pasanen-Mortensen et al., 2013). In terms of foxes, studies have shown that a low temperature may have a negative physiological impact (Bartoń & Zalewski, 2007; Pasanen-Mortensen et al., 2013). The temporal extent of snow cover has also been demonstrated to have a negative impact on fox density (Bartoń & Zalewski, 2007). Moreover, a high accumulation of snow during the winter may lead to difficulties for foxes to find prey as vole can benefit from these weather conditions by having an increased number of locations for concealment (Lindström & Hörnfeldt, 1994). Furthermore, snow depth also has an effect on the survival and reproduction of roe deer (Andrén & Liberg, 2015; Kjellander & Nordström, 2003). A correlation exists between harsh winters and increases in fox predation on roe deer as weak roe deer become a more vulnerable prey to foxes (Cederlund & Liberg, 1995; Cederlund & Lindström, 1983).

The aim of this study was to explore the factors affecting the dynamics of the fox population at Grimsö Wildlife Research Area in south-central Sweden. A comprehensive dataset over a temporal span of 51 years, including both top-down and bottom-up variables, was utilized to analyze the system prior, during and post-recolonization of apex predators (wolves and lynx).

Preceding the analysis, the following predictions were made:

1) Guided by both predictions and findings from research in Scandinavia and worldwide (Cavallini, 1996; Elmhagen et al., 2010; Helldin, 2004; Helldin et al., 2006; Lindström et al., 1994; Pasanen-Mortensen et al., 2013; Sunde et al., 1999; Wikenros et al., 2017), I predicted that there would be a decrease in the fox population after the recolonization of lynx and wolves, and that the most significant effect would be observed following lynx

arrival. Building further upon this (Newsome et al., 2017; Wikenros et al., 2017), I predicted that an increase in wolf pack size would have a prominent negative impact on the fox population.

2) In accordance to research regarding winter and its negative effect on fox populations (Andrén & Liberg, 2015; Bartoń & Zalewski, 2007; Kjellander & Nordström, 2003; Lindström, 1983; Pasanen-Mortensen et al., 2013; Lindström & Hörnfeldt, 1994), I predicted that there would be a decrease in the number of fox litters after harsh winters.
3) Given the research regarding sarcoptic mange and its effect on foxes (Danell & Hörnfeldt, 1987; Jarnemo & Liberg, 2005; Kjellander & Nordström, 2003; Lindström et al., 1994; Lindström & Mörner, 1985; Willebrand et al., 2022), I predicted that during the period that sarcoptic mange was prevalent in Grimsö Wildlife Research Area, there would be a decline in the fox population.
4) Drawing upon the relationship between voles and foxes (Kjellander & Nordström, 2003; Lindström 1988; Lindström 1989; Lindström & Mörner, 1985), I predicted that there would be a positive correlation between vole density and the fox population, and no temporal delay would be observed between the variables.
5) Hare and roe deer serve as an alternative prey resource (Angelstam et al., 1984; Cederlund & Lindström, 1983; Kjellander & Nordström, 2003) and previous studies have established that foxes can suppress these species (Aanes & Andersen, 1996; Elmhagen et al., 2010; Jarnemo & Liberg, 2005; Lindström et al., 1994). Based on this, I predicted that there would be a negative correlation between the abundance of foxes and the densities of hares and roe deer.
6) A system that is characterized by both bottom-up and top-down control should be affected by both apex predators and prey densities (Hunter & Price, 1992). Therefore, I predicted that there would be a positive correlation between the fox population size and the abundance of vole in the absence of apex predators and sarcoptic mange. However, when apex

predators and sarcoptic mange were present, there would be a decrease in the fox population.

2. Materials & methods

2.1 Study area

Grimsö Wildlife Research Area is located in south-central Sweden (59.73° N, 15.47° E), within the boreonemoral zone, residing in the region that has intermediate productivity (Lindström 1994). Topographically, the area is characterized by a low elevation reaching a maximum of 118 m.a.s.l (SITES, n.d.). It features flat ridges and large boulders (Cederlund et al., 1989). The landscape is defined by intensely managed forestry, with Scots pine (*Pinus silvestris*) and Norway spruce (*Picea abies*) as the predominant tree species, along with elements of birch (*Betula pubescens, B. pendula*) and aspen (*Populus tremula*) (Rönnegård et al., 2008). Arable land covers a small fraction of the area, and there is a considerable presence of bogs, mires and lakes (Kjellander et al., 2021).

2.2 Snow depth and temperature

Data on snow depth (meters) and minimum temperature (Celsius) from 1973 to 2024 were obtained from SMHI's weather station in Ställdalen. Measurements were made every day with some deviations when data was not available. Derived from this data, an average was calculated for each year by summarizing all values of snow depth divided by the number of days of the year based on daily measurements. An average of the temperature during the winter season each year was calculated by taking the mean of all the daily values of temperature between November – March (Barton & Zalewski 2007). Winter harshness was assessed according to the total amount of snow that fell during the year from the first day of fall to the last day of spring which varied every year and can be defined as a measure of the harshness of winter that year (Andrén & Liberg, 2015; Kjellander & Nordström, 2003).

2.3 Presence of apex predators

The Scandinavian wolf population has a history of persecution which culminated in the near extinction of the population, with approximately 10 individuals left in 1965 (Aronson & Sand, 2004; Wabakken et al., 2001). The following year, they were officially listed as protected, but by that time they were already considered to be “functionally extinct” (Wabakken et al., 2001). However, wolves from the Finnish-Russian population immigrated to Scandinavia, marking the beginning of the gradual yet consistent re-colonization of the population (Wabakken et al., 2001). The results from the annual monitoring in 2023-2024 estimated the part of the Scandinavian wolf population that are in Sweden to be a total of 375 individuals (95% CI = 296-487) (Wabakken et al., 2024).

Minimum and maximum number of wolves were compiled from the annual monitoring reports (Wabakken et al., 1999; Wabakken et al., 2024), where the re-establishment of wolves in Grimsö Wildlife ResearchArea occurred in 2003-2004 (Wabakken et al., 2004). Territorial pairs and family groups found in Uttersberg, Aspafallet, Hedbyn and Mjuggsjön territories were classified as present in the Grimsö Wildlife Research Area. From 2010-2011, the minimum and/or maximum number of individuals was no longer consistently estimated in Sweden. From 2011-2012 until 2014-2015, I used the minimum number of individuals reported, and from 2015-2016, I used two individuals for territorial pairs and assumed six individuals for family groups. In the case of multiple territories, the sum of the number of wolves were used. The pack size of the wolves has been estimated to range between a minimum of 2-9 individuals and a maximum of 2-12 individuals within the Grimsö Wildlife Research Area between the years 2003-2024 (Wabakken et al., 2004; Wabakken et al., 2024).

The Scandinavian lynx population also underwent a change within the same century resulting in a decrease in population size to a total of less than 100 individuals by 1920, and receiving protection eight years later (Spong & Hellborg 2002). The results from the annual monitoring 2023-2024 estimated the Swedish lynx population to be a total of 1276 individuals (95% CI = 1076-1477) (Tovmo & Frank 2024). The re-establishment of lynx in Grimsö Wildlife Research Area occurred around 1995-1996 (Andrén & Liberg, 2015).

2.4 Number of red fox litters and sarcoptic mange

The monitoring program at Grimsö Wildlife Research Area provided data on the number of fox litters. Annual inventories of fox litters have been carried out during May-June since 1973 (SITES, n.d.). The methodology consists of visiting all known dens, and upon discovery of pup scats or carcasses it is noted as a sign of reproductive activity (Andrén & Liberg 2015).

The first documented case of sarcoptic mange in Sweden occurred in 1972 and eight years later the fox population was severely affected nationally (Lindström & Mörner, 1985). The disease afflicted the population locally at Grimsö Wildlife Research Area between 1983-1989 which led to a reduction in the fox population size (Lindström et al., 1994). Although the disease may be more or less prevalent, it is during these years that the disease is considered to be present in this study whereas the years before and after it is considered to be absent (Kjellander & Nordström, 2003). According to bag records in Sweden, the recovery of Swedish fox populations is believed to have occurred during the late 1980s and early 1990s as there was an increase in the number of foxes being shot during this time (Willebrand et al., 2022). Research has later demonstrated a downward trend in the fox population at Grimsö Wildlife Research Area, a phenomenon that has been associated with the proliferation of the lynx population (Helldin et al., 2006).

2.5 Hare and roe deer indices

Pellet counts from roe deer and droppings from hares (*Lepus europaeus*, *Lepus timidus*) were derived from the annual inventory within the monitoring program at Grimsö Wildlife Research Area that was initiated in 1977 and has been carried out in April-May ever since (SITES, n.d.). The total number of sample sites are set out to be 2400 every year, however, due to the fact that some of the sites get damaged by wildlife and forest management, the exact number is generally a bit lower. The methodology of the inventory was modified in 1997, necessitating the need to use “method” as a factor in the statistical analyses to ascertain that the results were not influenced and skewed due to the use of different methods. The index used to test the effect of roe deer and hare was the number of pellet counts/droppings per area measured at 10 m^2.

2.6 Vole density

The estimation of vole density was derived from the spring index for bank vole and field vole trapped in snap traps over a period of 100 nights from the monitoring program within Grimsö Wildlife Research Area (SITES, n.d.). Approximately 950 traps distributed over 20 sampling sites covering 1 hectare have been set out every year for three nights in spring and fall at Grimsö Wildlife Research Area since 1973 (Andrén & Liberg, 2015; Kjellander & Nordström, 2003).

3.7 Statistical analysis

The initial step was to investigate the autocorrelation in order to determine if the number of fox litters are connected to previous years i.e. if time revealed a pattern in the population dynamics of fox. A lagged value for year t-1 was created using the package dplyr, and the correlation with the current year t was calculated. The function cor.test () was applied to test for statistical significance (P).

The model type used was a generalized linear model (GLM) with a Poisson distribution and logarithmic link function with the number of fox litters as the response variable and 11 predictor variables (listed in Table 1). Three datasets were created to perform the analysis, the first one contained data on the variables from the time period 1973-2024. However, in 1973, vole density exhibited an extreme value and was therefore excluded from the analysis after it was confirmed that it did not affect the result. I tested nine different models where vole density and sarcoptic mange were included in all the models in the complete dataset except for the null model. Three different indices for winter related to snow depth, temperature, and harshness were included in separate models in combination with vole density and sarcoptic mange. The presence of lynx and wolf were included in separate and combined models. Furthermore, a model that included the interaction between vole density and mange, as well as between wolf and mange was added. The rationale behind the exclusion of lynx in the interaction model was because this predictor variable showed no significant effect when all the variables were analyzed separately prior to creating the three datasets. See Table 2 for the different models that were tested.

In the aforementioned dataset, the predictor variables roe deer and hare density were not available during the first four years prior to 1977. Hence, the creation of a subset of data ranging between 1977-2024 was necessary. The winter variables were excluded in this dataset as well as the presence of lynx as those predictors were not important when analyzing the complete dataset (1974-2024). See Table 3 for the different models that were tested.

A third dataset was created to analyze the effect of wolf pack size. In addition to the null model, vole density was tested separately and in combination with the maximum number of wolf individuals per monitoring season (see Table 4). The models were compared using Akaike information criterion corrected for small sample sizes (AICc). The analysis was performed with RStudio version 4.3.1 (Posit Team, 2023).

Table 1. Overview of the dataset used in the analysis of the effect of top-down and bottom-up variables on fox litters at Grimsö Wildlife Research Area. The temporal span during which the data for the different predictor variables was available and used (ranging between 1974-2024) is listed. The type of data used and its source are listed as well.

Time period	Data type	Predictor variable	Source
1974 - 2024	Numeric	Vole density	Monitoring program within SITES
1974 - 2024	Numeric	Winter harshness	SMHI weather station in Ställdalen
1974 - 2024	Numeric	Snow depth	SMHI weather station in Ställdalen
1974 - 2024	Numeric	Minimum temperature	SMHI weather station in Ställdalen
1977 – 2024	Numeric	Roe deer density (mean no. of pellet counts	Monitoring program within SITES
1977 – 2024	Numeric	Hare density (mean no. of droppings)	Monitoring program within SITES
1977 – 2024	Factor (New/Old)	Inventory method	Monitoring program within SITES
1983 – 1989	Factor (1/0)	Sarcoptic mange (presence/absence)	Monitoring program within SITES
1995 – 2024	Factor (1/0)	Lynx (presence/absence)	Annual monitoring reports
2004-2024	Factor (1/0)	Wolf (presence/absence)	Annual monitoring reports

2004-2024	Numeric	Wolf pack size	Annual monitoring reports

Table 2. The selection of models based on the complete dataset (1974 – 2024) with top-down and bottom-up variables to test the effect on the fox population at Grimsö Wildlife Research Area. A total of nine models were chosen with the inclusion of vole density in all models and sarcoptic mange in eight out of nine models. The presence of lynx and wolf are included in separate models as well as combined. Snow depth, temperature and winter harshness are included in separate models and in combination with vole and sarcoptic mange.

Models	Predictor variables
Model 0	Null
Model 1	vole
Model 2	vole + mange
Model 3	vole + mange + wolf
Model 4	vole + mange + lynx
Model 5	vole + mange + wolf + lynx
Model 6	vole + mange + snow depth
Model 7	vole + mange + winter harshness
Model 8	vole + mange + winter temperature
Modell 9	vole + mange + wolf + vole * mange + vole * wolf

Table 3. The selection of models based on the subset of data (1977 - 2024) to test the effect of top-down and bottom-up variables on the fox population at Grimsö Wildlife Research Area with a total of five models, with the inclusion of vole and sarcoptic mange in all models. The effects of roe deer and hare densities are included in this dataset. The inventory was initiated in 1977, therefore these variables were not available in the complete dataset.

Models	Predictor variables
Model 0	Null
Model 1	vole + mange + roe deer + method
Model 2	vole + mange + hare + method
Model 3	vole + mange + wolf
Model 4	vole + mange + wolf + roe deer + method
Model 5	vole + mange + wolf + hare + method

Table 4. The selection of models to test the effect of wolf pack size (2004 – 2024) on the fox population at Grimsö Wildlife Research Area with a total of two models with the inclusion of vole in both models. The re-establishment of wolves occurred in 2003-2004, therefore the variable was not available in the other two datasets.

Models	**Predictor variables**
Model 0	Null
Model 1	vole
Model 2	vole + pack size

3. Results

From 1973-2024, the number of fox litters ranged between 1 to 10 (Appendix 1; Figure 1). In 1973-1982, before the presence of sarcoptic mange and apex predators, the mean number of fox litters was 6.6. During the years in which sarcoptic mange afflicted the fox population (1983-1989), the mean number of fox litters was 3.6. The lowest value, which was one litter, is concurrent with this period. After the reestablishment of apex predators (1995-2024), the mean number of fox litters was 5.3. These events are depicted in Figure 2 and 3.

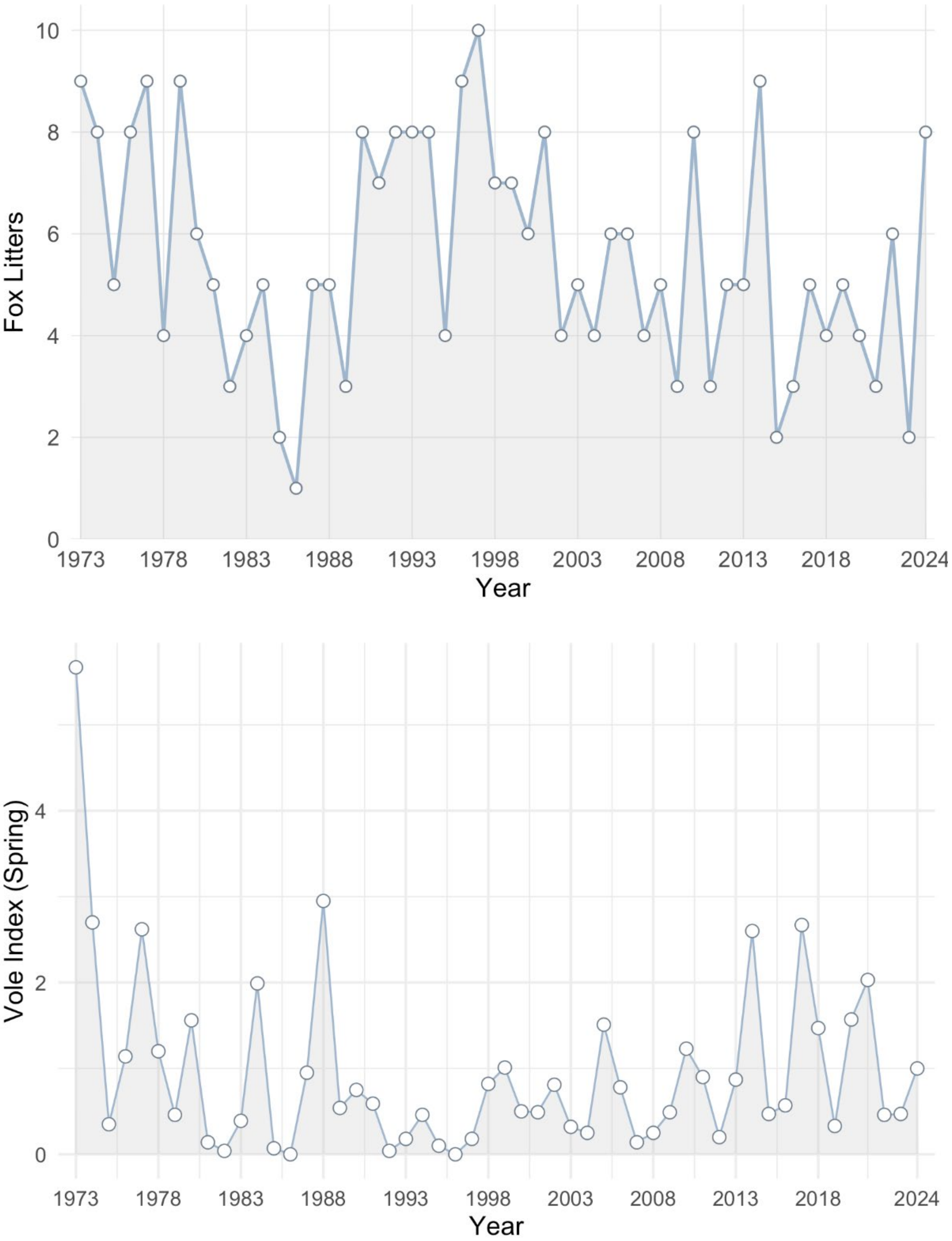

Figure 1. An overview of the number of fox litters observed over the period of 1973-2024 at Grimsö Wildlife Research Area in the upper graph. The lower graph depicts the annual index of voles during the period of 1973-2024 at Grimsö Wildlife Research Area showcasing the cyclicality of voles.

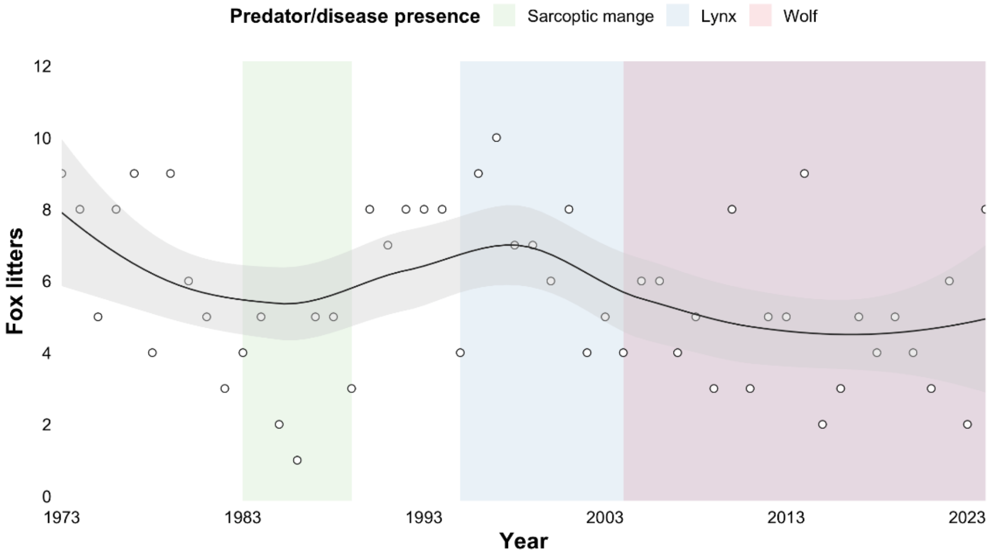

Figure 2. An overview of the number of fox litters during the time period 1973-2024 with three distinct events highlighted. Between the years 1983-1989, sarcoptic mange affected the fox population at Grimsö Wildlife Research Area and the period is depicted with a green shade. In 1995/1996, lynx recolonized Grimsö Wildlife Research Area, which is marked blue until 2003/2004 when the recolonization of wolves occurred, which is marked with pink and blocks out the blue color. Both of the apex predators are present at Grimsö Wildlife Research Area until the end of the study period (2024).

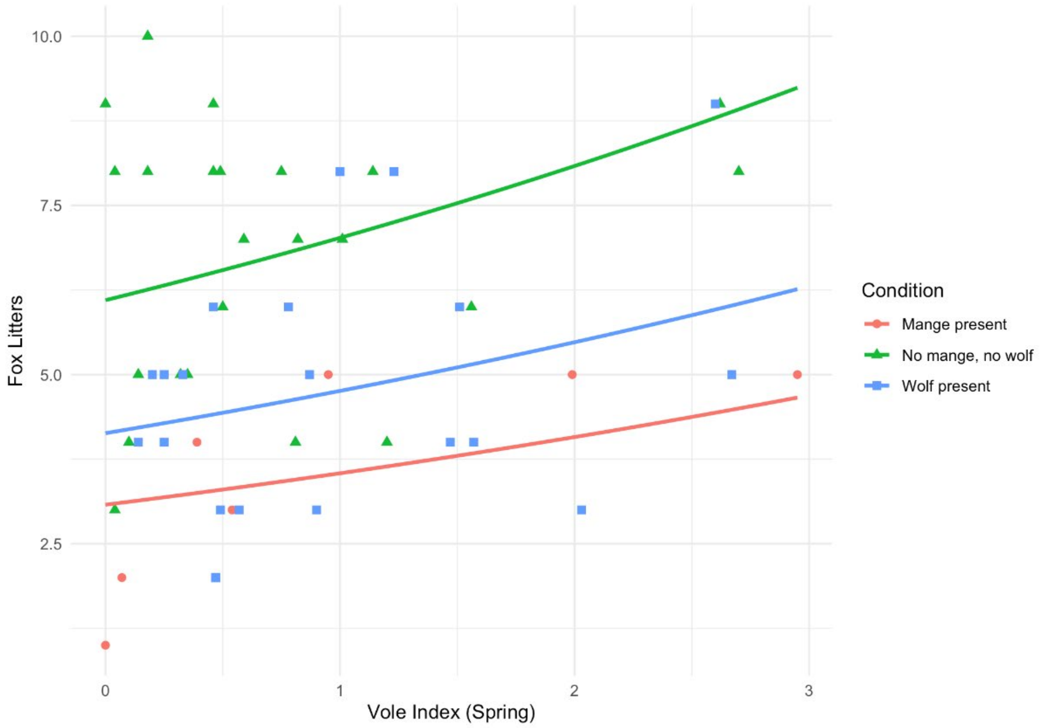

Figure 3. Scatterplot from a multiple regression with three lines describing the relationship between the number of fox litters and vole density during spring at Grimsö Wildlife Research Area in the years 1974-2024 during three different conditions. The green line and triangles represent when neither sarcoptic mange nor wolves were present in the area. The blue line and squares reflect the period between 2004-2024 when wolves are present. The red line and circles correspond to when sarcoptic mange was present, spanning from 1983-1989.

3.1 No random variation in fox litters

The autocorrelation analysis showed no correlation between fox litters year t and t-1 ($r = 0.14$, $df = 48$, $p = 0.34$) (Figure 4).

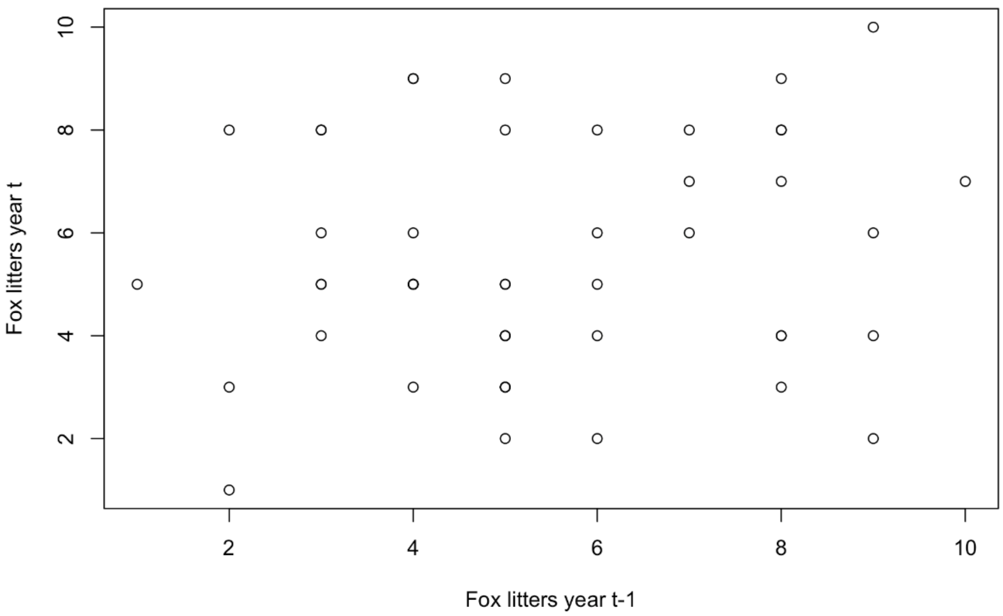

Figure 4. The correlation between fox litters year t and t-1 between the years 1973-2024 at Grimsö Wildlife Research Area.

3.2 Impact of top-down and bottom-up factors

The highest-ranking model in the complete dataset (1974-2024) included the variables vole density, sarcoptic mange, and wolf (Table 5). The presence of sarcoptic mange and wolf had a negative influence on the fox population, with sarcoptic mange being the predictor variable yielding the strongest slope (Table 6; Figure 5). The positive relationship between vole density and fox litters was almost statistically significant (p = 0.055).

Table 5. Generalized linear model on the complete dataset to test the correlation of top-down and bottom-up predictor variables on the fox population at Grimsö Wildlife Research Area during the years 1974-2024. Displaying all models that were tested including the null model.

Models	**AICc**	**ΔAICc**	**df**	**wi**
vole + mange + wolf	216.6	0.0	4	0.6336
vole + mange + lynx + wolf	219.0	2.4	5	0.1893
vole + mange + wolf + vole * mange + vole * wolf	220.4	3.9	6	0.0916
vole + mange + lynx	222.3	5.7	4	0.0360
vole + mange	223.4	6.9	3	0.0204
vole + mange + winter temperature	224.8	8.3	4	0.0102
vole + mange + winter harshness	225.6	9.0	4	0.0069
vole + mange + snow depth	225.7	9.1	4	0.0066
null	227.3	10.7	1	0.0030
vole	227.9	11.3	2	0.0022

Table 6. Estimate, standard error, Z value and p value for the highest-ranking model in the complete dataset, which incorporated top-down and bottom-up variables, to test the correlation of different predictor variables on the fox population at Grimsö Wildlife Research Area during the years 1974-2024.

Parameter	**Estimate**	**Std. Error**	**Z value**	**Pr (>|z|)**
intercept	1.81	0.0991	18.2	< 0.0001
vole	0.141	0.0735	1.92	0.055
mange	-0.684	0.217	-3.16	0.0016 **
wolf	-0.389	0.129	-3.01	0.0027 **

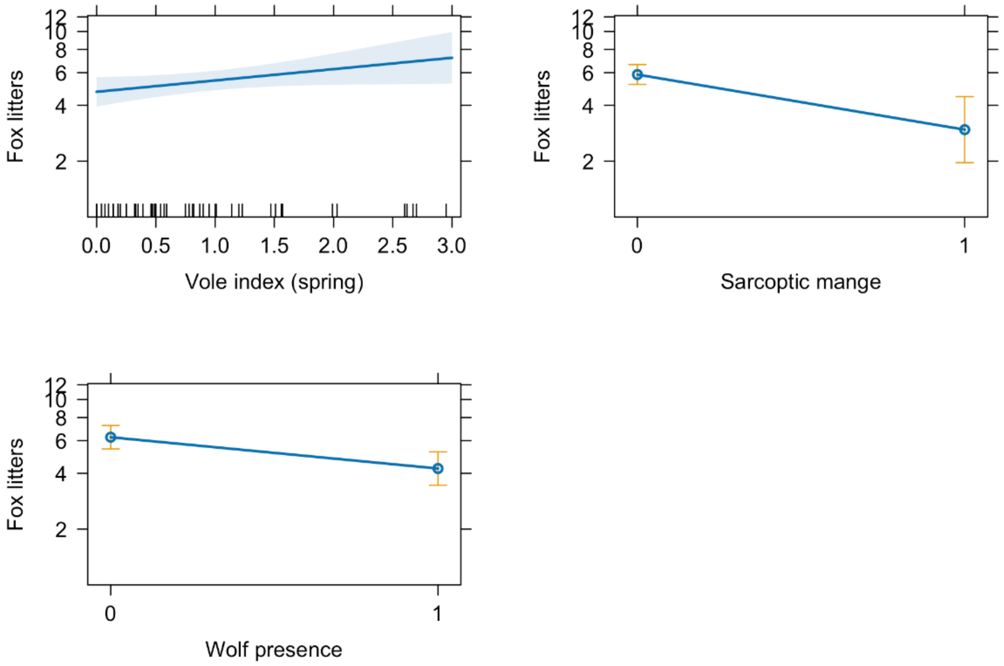

Figure 5. Line plots showing the correlation between the number of fox litters in relation to predictor variables at Grimsö Wildlife Research Area from the best model with the complete dataset between the years 1974-2024. The presence of sarcoptic mange and wolf had a significant negative effect. Vole density demonstrated a positive correlation with fox litters, almost attaining a statistically significant result. The blue shaded area highlights the confidence interval.

3.3 Impact of alternative prey

In the subset of the data from 1977, the model that attained the highest rank included the predictor variables vole, sarcoptic mange, and wolf presence on the number of fox litters (Table 7). Vole density had a significant positive correlation, in contrast to the presence of sarcoptic mange and wolf that had a significant negative effect (Table 8; Figure 6). There was no significant correlation between the number of fox litters and with hare and roe deer density indexes.

Table 7. Generalized linear model on the subset of data to test the correlation of top-down and bottom-up variables on the fox population at Grimsö Wildlife Research Area during the years 1977-2024. Displaying all models that were tested including the null model.

Models	**AICc**	**ΔAICc**	**df**	**wi**
vole + mange + wolf	204.0	0.0	5	0.737
vole + mange + wolf + hare + method	206.7	2.7	7	0.187
vole + mange + wolf + roe deer + method	209.2	5.3	7	0.052
vole + mange + hare + method	212.3	8.3	6	0.011
vole + mange + roe deer + method	212.4	8.4	6	0.011
null	217.4	13.4	2	<0.001

Table 8. Estimate, standard error, T value and p value for the highest-ranking model on the subset of data, which incorporated top-down and bottom-up variables, to test the correlation of different predictor variables on the fox population at Grimsö Wildlife Research Area during the years 1977-2024.

Parameter	**Estimate**	**Std. Error**	**T value**	**Pr (>|z|)**
intercept	1.804	0.0901	20.0	< 0.0001
vole	0.178	0.0692	2.57	0.014 *
mange	-0.748	0.158	-4.73	< 0.0001***
wolf	-0.424	0.114	-3.73	0.00055 ***

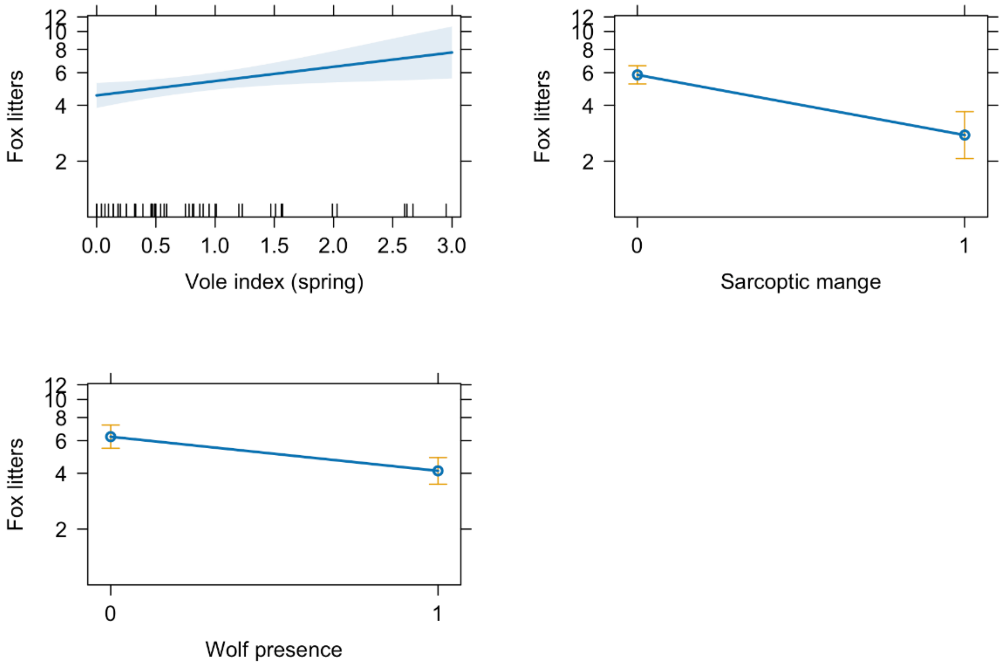

Figure 6. Line plots displaying the effect of predictor variables on the number of fox litters at Grimsö Wildlife Research Area from the best model using the subset of data between the years 1977-2024 including density of roe deer and hares, as the inventory of roe deer and hare was initiated in 1977 and those variables are therefore excluded from the complete dataset. The effect of vole density had a significant positive effect on fox litters, whereas the presence of sarcoptic mange and wolf had a significant negative effect. The blue shaded area highlights the confidence interval.

3.4 The impact of wolf pack size

The effect of wolf pack size did not influence the number of fox litters as it is the lowest ranking model out of the subset of data with no significant effect (Table 9, Figure 7). The estimate for vole in that model was 0.184, and the p-value was 0.16.

Table 9. Generalized linear model on the subset of data including wolf pack size during the years 2004-2023 at Grimsö Wildlife Research Area. The estimate for the null model was 1.56, std. error = 0.100, z value 15.6, p < 0.001.

Models	**AICc**	**ΔAICc**	**df**	**wi**
null	88.0	0.0	1	0.51
vole	88.5	0.6	2	0.39
vole + pack size	91.2	3.2	3	0.10

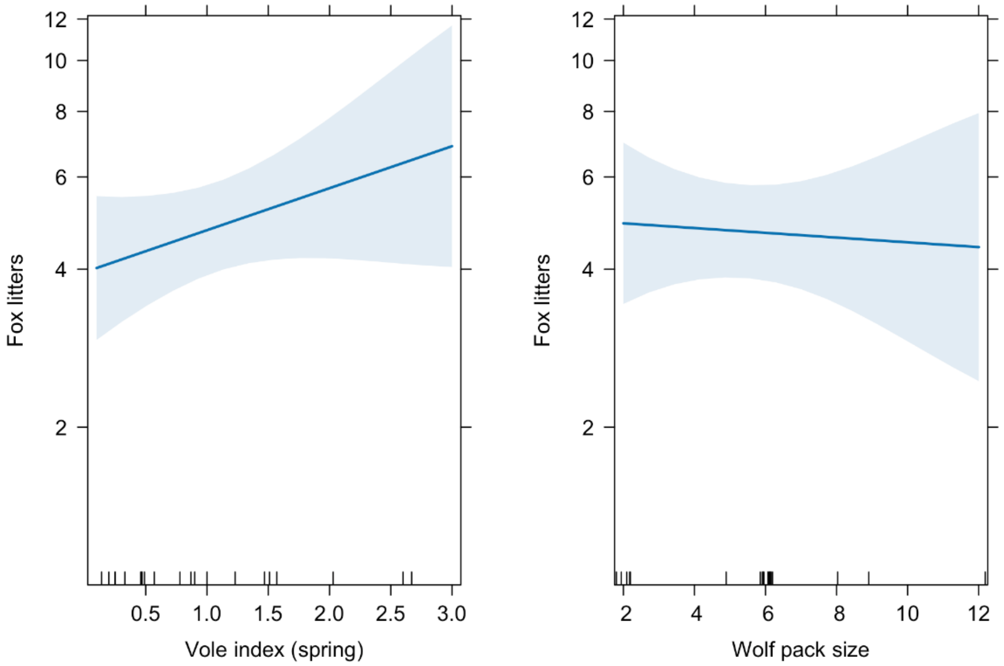

Figure 7. Line plots depicting the correlation between the number of fox litters in relation to vole density and wolf pack size at Grimsö Wildlife Research Area between the years 2004-2024. There was no significant correlation between fox litters and the aforementioned predictor variables. The blue shaded area highlights the confidence interval.

4. Discussion

4.1 Both top-down and bottom-up effects regulate fox density

The lack of autocorrelation indicates that other factors than previous year litter size are influencing the fox population in the Grimsö Wildlife Research Area as it is evident that a year with high number of litters not necessarily resulted in a high number the following year.

Through the analysis of long-term data collected over a period of five decades, I showed that the presence of sarcoptic mange and wolves has a negative influence on the fox population. These findings aligned with prediction 1 as well as research regarding the top-down effect apex predators exert on mesopredators (Cavallini, 1996; Elmhagen et al., 2010; Helldin, 2004; Helldin et al., 2006; Pasanen-Mortensen et al., 2013; Sunde et al., 1999; Wikenros et al., 2017). However, the wolf pack size did not have a significant effect on the fox population, as resulting from an analysis of a restricted dataset as supported by existing literature on the matter (Newsome et al., 2017; Wikenros et al., 2017). This may be due to that detailed information about wolf pack size within the study area was not available. Previous studies have demonstrated that the density of apex predators typically has an impact on the fox population (Newsome et al., 2017; Stephenson et al., 1991; reviewed in Ritchie & Johnson, 2009; Wikenros et al., 2017). In another study in Sweden, Wikenros et al., (2017) found that there was a negative correlation between fox abundance and wolf pack size. In addition, the magnitude of this phenomenon was most prominent two years after the establishment of wolf packs. However, they found no correlation between fox abundance and wolf occurrence at a landscape scale.

In Alaska, Stephenson et al., (1991) posited that when lynx reaches high density, they can suppress foxes. My study did not find a negative relationship between the presence of lynx and the fox population, which stands in contrast to my prediction regarding that the greatest impact from apex predators would come from lynx. A multitude of studies have consistently demonstrated a negative relationship between the two species in question (Elmhagen & Rushton, 2007; Elmhagen et al., 2010; Helldin et al., 2006; Helldin, 2004; Stephenson et al., 1991). At Grimsö Wildlife Research Area, Helldin et al., (2006) demonstrated that in the aftermath of the establishment of lynx, there was a decline in the number of fox litters and observations of foxes. Notably, this decline occurred before the establishment of wolves which is also evident in this study (see Figure 2). Intraguild predation was confirmed through radio tracking of foxes and snow tracking of lynx, and the predation appeared to be additive to some degree (Helldin et al., 2006). The methods used in this study versus Helldin et al., (2006) are not directly comparable due to temporal differences and the type of data used. Specifically, I analyzed the direct relationship between variables, while Helldin et al., (2006) incorporated a time lag. Hence, the discrepancy in results may be explained by this factor. Also, there is a temporal overlap between the presence of lynx and wolves in the study area, and therefore it is valid to postulate that the cumulative effect of both predators may have contributed to the decline of the fox population.

In the analysis, there were three predictor variables connected to winter: temperature, snow depth and winter harshness. None of them had a significant effect on the fox population, which contradicts prediction 2. However, winter has been shown to be one of the major factors influencing the density of fox populations in Eurasia (reviewed in Barton & Zalewski 2007). The lack of effect in this present study may be due to the spatial scale, as it was conducted at a local level. In contrast, the review by Barton & Zalewski (2007) included studies that covered an extensive geographical range.

There was a positive correlation between vole density and the fox population, thus supporting prediction 4. In literature, this relationship is well-documented (Kjellander & Nordström, 2003; Lindström 1988; Lindström & Mörner, 1985). Specifically, the mean litter size of the red fox has been attributed to vole density (Englund 1970; Lindström 1988).

There was no evidence that suggests a negative correlation between increased fox density and the density of hares and roe deer, which contrasts with prediction 5. Lindström et al., (1994) demonstrated that during the years that sarcoptic mange was prevalent in the Grimsö Wildlife Research Area, mountain hares increased up to 100%. Indeed, subsequent to the recovery of the fox population, the hare population decreased. Moreover, roe deer fawns have shown to be vulnerable to predation from foxes (Aanes & Andersen, 1996; Cederlund & Lindström, 1983; Jarnemo & Liberg, 2005), especially when the abundance of vole is low (Kjellander & Nordström, 2003). A possible cause for the imperceptible effect on prey species in this study may be because of the temporal delay between the fox population and the level of predation pressure on roe deer fawns (Kjellander & Nordström, 2003), which was not included in this study. In addition, the lack of effect could be due to the selected index for roe deer which was mean number of pellet piles per year. An index based on roe deer fawns may have yielded different results, as red fox primarily targets fawns rather than adults (Cederlund & Lindström, 1983).

Concerning the matter of whether bottom-up, top-down or both bottom-up and top-down factors influences the fox population, the results are in agreement with a combination of both factors. As indicated in Figure 3, the relationship between the fox population and vole density followed the same pattern in the absence and presence of apex predators and sarcoptic mange, however with a marked decrease in the number of fox litters. These observations suggest that the fox population is constrained by both bottom-up (vole) and top-down (wolves, mange) factors in accordance with prediction 8.

4.2 Strengths and weaknesses

This study had strengths in the form of access to long-term data on apex predators, mesopredator and its prey which is noteworthy for its rarity (Beschta & Ripple, 2009; Richie & Johnson). Furthermore, the time period during this study included data prior, concurrent and subsequent to apex predators' presence which could be viewed as a "semi-natural experiment" which may facilitate more precise discernment of effects (Cavallini, 1996; Estes et al., 2011).

The approach to include variables that represented top-down and bottom-up processes offered a distinct advantage, given these processes' ability to shape the structure of ecosystems. To exclude one of these processes would have led to an incomplete understanding of the comprehensive dynamics of ecosystems (Richie & Johnson 2009). A notable weakness in this study was the decision to not include arable land as a variable in the analysis, which have been recognized to be a pivotal factor influencing fox abundance (Wikenros et al., 2017). The rationale behind this was due to the small fraction of arable land in the study area and the knowledge that there has been negligible change during the years.

The use of direct relationship between the variables is comparatively simple to the methodology of incorporating a time lag and was proven to be sufficient to demonstrate that there is a correlation between top-down and bottom-up variables and the number of fox litters at Grimsö Wildlife Research Area.

However, the findings of previous studies that utilized parts of the same dataset and demonstrated a significant correlation between roe deer and hare density as well as the presence of lynx underscores the importance to incorporate a time lag.

No data on the density of lynx in Grimsö Wildlife Research Area was available in addition to the lack of density data for wolves within the study area. Access to detailed density data of both the apex predators would have improved the study.

The present study is confined to a single study area, however, due to the rarity of the time series, it provides unique results.

4.3 Future studies

A species that merits further research in relation to the dynamics of the red fox is the pine marten. During the sarcoptic mange outbreak, the pine marten population grew which has been linked to the decrease of foxes (Lindström et al., 1994; Storch et al., 1990).

As previously stated in regard to fox predation on roe deer, future studies would do well to incorporate a time lag when testing for a density correlation between the two species. The reduction in the roe deer population is anticipated to occur in the subsequent years following a decline in vole density as a result of prey switching by foxes from voles to roe deer fawns. Another refinement would be to change the response variable from fox to roe deer and for predictor variables have vole, snow depth and harvest with the inclusion of a time lag. It is plausible to hypothesize that this would lead to an indirect positive effect on the number of fox litters. A comparable result may be observed by using hare density as response variable and for predictor variables have vole, lynx and grouse also with the inclusion of a time lag.

Detailed data on the density of wolf and lynx offers the opportunity to test the enemy constraint hypothesis. Testing the validity of this relationship between these species would offer valuable insight on their ecological dynamics. In addition, individual characteristics of wolves may be of value to include as predictor variables such as age and gender as this has been proven to matter when it comes to hunting success on moose. Older male wolves have much higher hunting success than younger male wolves, whereas the same conclusions could not be drawn for female age (Sand et al., 2006).

5. Conclusion

To conclude, the findings of this study showed that sarcoptic mange exerted a substantial negative impact on the fox population at Grimsö Wildlife Research Area during its prevalence in the 1980s. Moreover, it was shown that voles remain to be a beneficial food resource for foxes. There is also strong indication that the most significant negative impact from apex predators stems from the presence of wolves, which has received less empirical validation in extant research. However, lynx most likely lowered the fox population when establishing before wolves where the latter kept the fox population at a lower level. To confirm this, a time lag should have been considered in the analysis. Thus, the fox population is limited by both bottom-up and top-down forces. The findings from this study may be valuable from a conservation point of view as the return of apex predators may result in cascading effects that benefit lower trophic levels, potentially promoting biodiversity (Palomares & Caro 1998). Future studies on fox decline should therefore consider sarcoptic mange, the presence of apex predators, and vole density as influential factors for fox populations.

References

Aanes, R., & Andersen, R. (1996). The effects of sex, time of birth, and habitat on the vulnerability of roe deer fawns to red fox predation. *Canadian Journal of Zoology*, *74*(10), 1857-1865.

Andrén, H., & Liberg, O. (2015). Large Impact of Eurasian Lynx Predation on Roe Deer Population Dynamics. *PLOS One*.

Aronson, Å., & Sand, H. (2004). *Om vargens utveckling i Skandinavien under de senaste 30 åren. III*. https://res.slu.se/id/publ/3881

Artfakta från SLU Artdatabanken. (n.d.). Retrieved May 18, 2025, from https://artfakta.se/taxa/206026

Bartoń, K. A., & Zalewski, A. (2007). Winter severity limits red fox populations in Eurasia. *Global Ecology and Biogeography*, *16*(3), 281–289. https://doi.org/10.1111/j.1466-8238.2007.00299.x

Beschta, R. L., & Ripple, W. J. (2009). Large predators and trophic cascades in terrestrial ecosystems of the western United States. *Biological Conservation*, *142*(11), 2401–2414. https://doi.org/10.1016/J.BIOCON.2009.06.015

Cavallini, P. (1996). Variation in the social system of the red fox. *Ethology Ecology & Evolution*, *8*(4), 323–342. https://doi.org/10.1080/08927014.1996.9522906

Cederlund, G., & Liberg, O. (1995). *Rådjuret: viltet, ekologin och jakten*. Svenska jägareförbundet.

Cederlund, G., & Lindström, E. (1983). Effects of severe winters and fox predation on roe deer mortality. *Http://Katalog.Pan.Pl/Webpac-Bin/223bzbsPL/Wgbroker.Exe?New+-Access+top+search+open+NR+ee95400552*, *28*(7), 129–145. https://doi.org/10.4098/AT.ARCH.83-9

Cederlund, G. N., Bergström, R. L., & Danell, K. (1989). Seasonal Variation in Mandible Marrow Fat in Moose. In *Source: The Journal of Wildlife Management* (Vol. 53, Issue 3). https://about.jstor.org/terms

Danell, K., & Hörnfeldt, B. (1987). Numerical responses by populations of red fox and mountain hare during an outbreak of sarcoptic mange. *Oecologia*, *73*(4), 533–536. https://doi.org/10.1007/BF00379412/METRICS

Elmhagen, B., Ludwig, G., Rushton, S. P., Helle, P., & Lindén, H. (2010). Top predators, mesopredators and their prey: interference ecosystems along bioclimatic productivity gradients. *Journal of Animal Ecology*, *79*(4), 785–794. https://doi.org/10.1111/J.1365-2656.2010.01678.X

Elmhagen, B., & Rushton, S. P. (2007). Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecology Letters*, *10*(3), 197–206. https://doi.org/10.1111/J.1461-0248.2006.01010.X

Englund, J. (1980). Population Dynamics of the Red Fox (Vulpes vulpes L., 1758) in Sweden. *The Red Fox*, 107–121. https://doi.org/10.1007/978-94-017-5592-4_9

Englund, J. 1970. Some aspects of reproduction and mortality rates in Swedish foxes (Vulpes vulpes) 1961-63 and 1966-69. - Viltrevy 8: 1

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., C Jackson, J. B., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., … Virtanen, R. (2011). Trophic Downgrading of Planet Earth. In *New Series* (Vol. 333, Issue 6040). https://doi.org/10.1126/science.1205106

Fretwell, S. D., & Barach, A. L. (1977). The Regulation of Plant Communities by the Food Chains Exploiting Them. *Perspectives in Biology and Medicine*, *20*(2), 169–185. https://doi.org/10.1353/pbm.1977.0087

Grimsö Wildlife Research Station (2025). Fox reproduction from Grimsö, Centroid of Research Area, 1973–2024 [Data set]. Swedish Infrastructure for Ecosystem Science (SITES). https://hdl.handle.net/11676.1/xvXFWr8Q-wTZZU9A8lRp9393

Grimsö Wildlife Research Station (2025). Pellet counts and Habitat survey from Grimsö, Centroid of Research Area, 1997–2025 [Data set]. Swedish Infrastructure for Ecosystem Science (SITES). https://hdl.handle.net/11676.1/V-Gf_0cFk9wyJ2QXFCuBqCVR

Grimsö Wildlife Research Station (2025). Small rodent dynamics from Grimsö, Centroid of Research Area, 1973-05-01–2024-09-30 [Data set]. Swedish Infrastructure for Ecosystem Science (SITES). https://hdl.handle.net/11676.1/SSmJvPK_dJ5GZq7an2y2zzJp

Helldin, Danielsson, & Anna V. (2007). *Changes in red fox Vulpes vulpes diet due to colonisation by lynx Lynx lynx*. https://doi.org/10.2981/0909

Helldin, J. O., Liberg, O., & Glöersen, G. (2006). Lynx (Lynx lynx) killing red foxes (Vulpes vulpes) in boreal Sweden - Frequency and population effects. *Journal of Zoology*, *270*(4), 657–663. https://doi.org/10.1111/j.1469-7998.2006.00172.x

Helldin, J.-O. (2004). *Lodjurspredation på räv – och dess sekundära effekter på bytespopulationerna. – Slutrapport, Grimsö forskningsstation, SLU.*

Hunter, M. D., & Price, P. W. (1992). Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology*, *73*(3), 724–732. https://doi.org/10.2307/1940152

Jachowski, D. S., Butler, A., Eng, R. Y. Y., Gigliotti, L., Harris, S., & Williams, A. (2020). Identifying mesopredator release in multi-predator systems: a review of evidence from North America. *Mammal Review*, *50*(4), 367–381. https://doi.org/10.1111/MAM.12207

Jaktlag (1987:259) | Sveriges riksdag. (n.d.). Retrieved May 18, 2025, from https://www.riksdagen.se/sv/dokument-och-lagar/dokument/svensk-forfattningssamling/jaktlag-1987259_sfs-1987-259/

Jarnemo, A., & Liberg. (n.d.). RED FOX REMOVAL AND ROE DEER FAWN SURVIVAL-A 14-YEAR STUDY. *Source: Journal of Wildlife Management*, *69*(3), 1090–1098. https://doi.org/10.2193/0022

Jędrzejewski, W., Jędrzejewska, B., & Szymura, A. (1989). Food Niche Overlaps in a Winter Community of Predators in the Białowieża Primeval Forest, Poland. *Acta Theriologica*, *34*, 487–496. https://doi.org/10.4098/AT.ARCH.89-48

Kjellander, P. L., Aronsson, M., Bergvall, U. A., Carrasco, J. L., Christensson, M., Lindgren, P. E., Åkesson, M., & Kjellander, P. (2021). Validating a common tick survey method: cloth-dragging and line transects. *Experimental and Applied Acarology*, *83*(1), 131–146. https://doi.org/10.1007/s10493-020-00565-4

Kjellander, P., & Nordström, J. (2003). Cyclic voles, prey switching in red fox, and roe deer dynamics – a test of the alternative prey hypothesis. *Oikos*, *101*(2), 338–344. https://doi.org/10.1034/J.1600-0706.2003.11986.X

Lariviere, S., & Pasitschniak-Arts, M. (1996). *Vulpes vulpes* (Vol. 3, Issue 537). https://about.jstor.org/terms

Lindström, E. (1982). *POPULATION ECOLOGY OF THE RED FOX (VULPES VULPES L.) IN RELATION TO FOOD SUPPLY*.

Lindström, E. (1983). Condition and growth and Red Foxes (Vulpes vulpes) in relation to food supply. *Journal of Zoology*, *199*(1), 117–122. https://doi.org/10.1111/J.1469-7998.1983.TB06120.X

Lindström, E., & Lindstrom, E. (1988). Reproductive Effort in the Red Fox, Vulpes vulpes, and Future Supply of a Fluctuating Prey. *Oikos*, *52*(1), 115. https://doi.org/10.2307/3565990

Lindström, E., & Mörner, T. (1985). The spreading of sarcoptic mange among swedish Red foxes (Vulpes vulpes L) in relation to Fox population dynamics. *Revue d'Écologie (La Terre et La Vie)*, *40*(2), 211–216. https://doi.org/10.3406/REVEC.1985.6585

Lindström, E. R. (1994). *Large Prey for Small Cubs: On Crucial Resources of a Boreal Red Fox Population* (Vol. 17, Issue 1). https://www.jstor.org/stable/3682929

Lindstrom, E. R., Andren, H., Angelstam, P., Cederlund, G., Hornfeldt, B., Jaderberg, L., Lemnell, P. A., Martinsson, B., Skold, K., & Swenson, J. E. (1994). Disease reveals the predators: Sarcoptic mange, red fox predation, and prey populations. *Ecology*, *75*(4), 1042–1049. https://doi.org/10.2307/1939428

Lindström, E. R., Hörnfeldt, B., Lindstrom, E. R., & Hornfeldt, B. (1994). Vole Cycles, Snow Depth and Fox Predation. *Oikos*, *70*(1), 156. https://doi.org/10.2307/3545711

MacArthur, R. H. (1972). Strong, or weak, interactions. *Transactions of the Connecticut Academy of Arts and Sciences*, *44*(177), 88.

Mittelbach, G. G., Osenberg, C. W., & Leibold, M. A. (1988). Trophic Relations and Ontogenetic Niche Shifts in Aquatic Ecosystems. *Size-Structured Populations*, 219–235. https://doi.org/10.1007/978-3-642-74001-5_15

Newsome, T. M., Greenville, A. C., Ćirović, D., Dickman, C. R., Johnson, C. N., Krofel, M., Letnic, M., Ripple, W. J., Ritchie, E. G., Stoyanov, S., & Wirsing, A. J. (2017). Top predators constrain mesopredator distributions. *Nature Communications 2017 8:1*, *8*(1), 1–7. https://doi.org/10.1038/ncomms15469

Oksanen, L., Fretwell, S. D., Arruda, J., & Niemelä, P. (1981). Exploitation Ecosystems in Gradients of Primary Productivity. In *Source: The American Naturalist* (Vol. 118, Issue 2). https://www.jstor.org/stable/2460513

Oksanen, L., & Oksanen, T. (2000). The logic and realism of the hypothesis of exploitation ecosystems. *American Naturalist*, *155*(6), 703–723. https://doi.org/10.1086/303354

Paine, R. T. (1980). Food webs: linkage, interaction strength and community infrastructure. *Journal of animal ecology*, *49*(3), 667-685. https://doi-org.ezproxy.its.uu.se/10.2307/4220

Pasanen-Mortensen, M., Pyykönen, M., & Elmhagen, B. (2013). Where lynx prevail, foxes will fail – limitation of a mesopredator in Eurasia. *Global Ecology and Biogeography*, *22*(7), 868–877. https://doi.org/10.1111/GEB.12051

Posit team (2023). RStudio: Integrated Development Environment for R. Posit Software, PBC, Boston, MA. URL http://www.posit.co/

Power, M. E. (1992). Top-down and bottom-up forces in food webs: do plants have primacy. *Ecology*, *73*(3), 733-746.

Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, *12*(9), 982–998. https://doi.org/10.1111/J.1461-0248.2009.01347.X

Rönnegård, Lars, J., & Pehrson. (n.d.). *Evaluation of four methods used to estimate population density of moose Alces alces*. https://doi.org/10.2981/0909

Sand, H., Wikenros, C., Wabakken, P., & Liberg, O. (2006). Effects of hunting group size, snow depth and age on the success of wolves hunting moose. Animal behaviour, 72(4), 781-789. https://doi.org/10.1016/j.anbehav.2005.11.030

Scholz, C., Firozpoor, J., Kramer-Schadt, S., Gras, P., Schulze, C., Kimmig, S. E., Voigt, C. C., & Ortmann, S. (2020). Individual dietary specialization in a generalist predator: A stable isotope analysis of urban and rural red foxes. *Ecology and Evolution*, *10*(16), 8855–8870. https://doi.org/10.1002/ECE3.6584

Soulé, M. E., Bolger, D. T., Alberts, A. C., Wrights, J., Sorice, M., & Hill, S. (1988). Reconstructed Dynamics of Rapid Extinctions of Chaparral-Requiring Birds in Urban Habitat Islands. *Conservation Biology*, *2*(1), 75–92. https://doi.org/10.1111/J.1523-1739.1988.TB00337.X

Sovada, M. A., Sargeant, A. B., & Grier, J. W. (1995). Differential Effects of Coyotes and Red Foxes on Duck Nest Success. *The Journal of Wildlife Management*, *59*(1), 1. https://doi.org/10.2307/3809108

Stephenson, R., Grangaard, D., & Burch, J. (1991). Lynx (Felix lynx) predation on red foxes (Vulpes vulpes), Caribou (Rangifer tarandus), and dall sheep (Ovis dalli) in Alaska. *Can. Field-Nat.*

Storch, I., Lindstrom, E., & de JOUNGE, J. (1990). Diet and habitat selection of the pine marten in relation to competition with the red fox. Acta Theriologica, 35(3-4).

Sunde, P., Overskaug, K., & Kvam, T. (1999). Intraguild predation of lynxes on foxes: evidence of interference competition? *Ecography*, *22*, 521–523. https://www.jstor.org/stable/3683144

Terborgh, J., Estes, J. E., Paquet, P., Ralls, K., Boyd-Herger, D., Miller, B. J., & Noss, R. F. (1999). *The role of top carnivores in regulating terrestrial ecosystems* (pp. 39–64).

The Swedish Infrastructure for Ecosystem Science | SITES. (n.d.). Retrieved May 18, 2025, from https://www.fieldsites.se/

Tovmo, M. & Frank, J. 2024. Bestandsovervåking av gaupe i 2024. Inventering av lodjur 2024. Bestandsstatus for store rovdyr i Skandinavia. Beståndsstatus för stora rovdjur i Skandinavien. Nr 2-2024. 33 s.

van Schaik, T., van Kuijk, M., & Sterck, E. H. M. (2025). Understanding mesopredator responses to changes in apex predator populations in Europe: implications for the mesopredator release hypothesis. *Mammal Review*, *55*(1), e12357. https://doi.org/10.1111/MAM.12357

Wabakken, P., Aronson, Å., Sand, H., Steinset, O. K. & Kojola, I. 1999. Ulv i Skandinavia: Statusrapport for vinteren 1998-99. Høgskolen i Hedmark, rapp. 19/99. 46s.

Wabakken, P., Aronson, Å., Sand, H., Steinset, O.K. & Kojola, I. 2001. Ulv i Skandinavia. Statusrapport for vinteren 2000-2001.- Oppdragsrapport nr. 1 - 2001. Høgskolen i Hedmark.

Wabakken, P., Aronson, Å., Sand, H., Strømseth, T. H., & Kojola, I. (2004). *Ulv i Skandinavia: Statusrapport for vinteren 2003-2004*.

Wabakken, P., Svensson, L., Maartmann, E., Nordli, K., Flagstad, Ø., Danielsson, A., Cardoso Palacios, C., & Åkesson, M. (2024). Bestandsovervåking av ulv vinteren 2023-2024. *60*. https://brage.nina.no/nina-xmlui/handle/11250/3131698

Walton, Z., Samelius, G., Odden, M., & Willebrand, T. (2017). Variation in home range size of red foxes Vulpes vulpes along a gradient of productivity and human landscape alteration. *PLOS ONE*, *12*(4), e0175291. https://doi.org/10.1371/JOURNAL.PONE.0175291

Weber, J. M., & Meia, J. S. (1996). Habitat use by the red fox Vulpes vulpes in a mountainous area. *Ethology Ecology & Evolution*, *8*(3), 223–232. https://doi.org/10.1080/08927014.1996.9522914

Wikenros, C., Aronsson, M., Liberg, O., Jarnemo, A., Hansson, J., Wallgren, M., Sand, H., & Bergström, R. (2017). Fear or food - Abundance of red fox in relation to occurrence of lynx and Wolf. *Scientific Reports*, *7*(1). https://doi.org/10.1038/s41598-017-08927-6

Wikenros, C., Sand, H., Ahlqvist, P., & Liberg, O. (2013). Biomass Flow and Scavengers Use of Carcasses after Re-Colonization of an Apex Predator. *PLOS ONE*, *8*(10), e77373. https://doi.org/10.1371/JOURNAL.PONE.0077373

Wikenros, C., Ståhlberg, S., & Sand, H. (2014). Feeding under high risk of intraguild predation: Vigilance patterns of two medium-sized generalist predators. *Journal of Mammalogy*, *95*(4), 862–870. https://doi.org/10.1644/13-MAMM-A-125/2/JMAMMAL-95-4-862-FIG3.JPEG

Willebrand, T., Samelius, G., Walton, Z., Odden, M., & Englund, J. (2022). Declining survival rates of red foxes Vulpes vulpes during the first outbreak of sarcoptic mange in Sweden. *Wildlife Biology*, *2022*(1), e01014. https://doi.org/10.1002/WLB3.01014

Wilmers, C. C., Post, E., Peterson, R. O., & Vucetich, J. A. (2006). Predator disease out-break modulates top-down, bottom-up and climatic effects on herbivore population dynamics. *Ecology Letters*, *9*(4), 383–389. https://doi.org/10.1111/J.1461-0248.2006.00890.X

Popular science summary

The red fox is among the most widespread species of mammals worldwide and they are found throughout Sweden. However, the population at Grimsö Wildlife Research Area in Bergslagen, has declined during the last decades.

The return of wolf and lynx in the area have contributed to the decline. Scabies also have an important role in their survival. Small rodents continue to be a significant food source, as their peak seasons coincides with periods when the fox population is also high. This indicates that access to this food source boosts the growth of the fox population. However, the correlation is weaker when top predators are in the area. This indicates that top predators affect how well the fox can utilize their prey.

The study shows that the fox population at Grimsö Wildlife Research Area is limited by forces above, in the form of top predators and disease, and below through the access of prey. This population is an example of how multiple ecological forces can occur at the same time in nature.

Understanding these interactions is important, as the return of large predators can create cascading effects in the ecosystem and contribute to greater biodiversity.

Acknowledgements

I thank my supervisor Camilla Wikenros, firstly for an inspiring lecture that brought this idea of a thesis to life and then for agreeing to take me under your wings and creating this project. I am grateful for your insightful guidance and unwavering support. I thank my assistant supervisor, Henrik Andrén, for agreeing to be involved in this project despite having a well-deserved retirement just around the corner. I am grateful for your wise guidance and support, especially with regard to statistics. I thank my examiner Håkan Sand. Your thorough review has elevated the quality of the manuscript and have offered opportunities for academic growth. I thank my opponent Amanda Silwer. Your feedback has been helpful and have given me new perspectives. All of the above have dedicated a great deal of time and effort to provide valuable comments and thoughts which have led to substantial improvements to the final version of the manuscript. This master thesis has been made possible by the Swedish Infrastructure for Ecosystem Science (SITES), in this case at Grimsö Wildlife Research Station, as well as data from annual monitoring of wolves and lynx.

6. Appendix 1

Data on estimates of population densities of red fox, vole, roe deer and mountain hare used in this study are presented herein, as well as the pack size of wolves and the presence/absence of wolf, lynx and sarcoptic mange in Grimsö Wildlife Research Area during the period 1973–2024. Furthermore, data on snow depth and winter temperature from SMHI’s weather station in Ställdalen are provided in meters and Celsius.

Year	**Fox litter**	**Wolf presence**	**Wolf individuals min**	**Wolf individuals max**	**Lynx presence**	**Vole index spring**
1973	9	0	0	0	0	5.67
1974	8	0	0	0	0	2.7
1975	5	0	0	0	0	0.35
1976	8	0	0	0	0	1.14
1977	9	0	0	0	0	2.62
1978	4	0	0	0	0	1.2
1979	9	0	0	0	0	0.46
1980	6	0	0	0	0	1.56
1981	5	0	0	0	0	0.14
1982	3	0	0	0	0	0.04
1983	4	0	0	0	0	0.39
1984	5	0	0	0	0	1.99
1985	2	0	0	0	0	0.07
1986	1	0	0	0	0	0.00
1987	5	0	0	0	0	0.95
1988	5	0	0	0	0	2.95
1989	3	0	0	0	0	0.54
1990	8	0	0	0	0	0.75
1991	7	0	0	0	0	0.59
1992	8	0	0	0	0	0.04
1993	8	0	0	0	0	0.18
1994	8	0	0	0	0	0.46
1995	4	0	0	0	1	0.1

1996	9	0	0	0	1	0.00
1997	10	0	0	0	1	0.18
1998	7	0	0	0	1	0.82
1999	7	0	0	0	1	1.01
2000	6	0	0	0	1	0.5
2001	8	0	0	0	1	0.49
2002	4	0	0	0	1	0.81
2003	5	0	0	0	1	0.32
2004	4	1	2	2	1	0.25
2005	6	1	5	6	1	1.51
2006	6	1	9	9	1	0.78
2007	4	1	4	6	1	0.14
2008	5	1	2	2	1	0.25
2009	3	1	4	5	1	0.49
2010	8	1	2	2	1	1.23
2011	3	1	2	2	1	0.9
2012	5	1	3	6	1	0.2
2013	5	1	4	6	1	0.87
2014	9	1	6	8	1	2.6
2015	2	1	7	12	1	0.47
2016	3	1	2	2	1	0.57
2017	5	1	6	6	1	2.67
2018	4	1	6	6	1	1.47
2019	5	1	6	6	1	0.33
2020	4	1	6	6	1	1.57
2021	3	1	6	6	1	2.03
2022	6	1	6	6	1	0.46
2023	2	1	6	6	1	0.47
2024	8	1	6	6	1	1.00

Year	Roe deer pellet mean no pellet piles	Roe deer % plots with pellet piles	Hare pellet mean no pellet piles	Hare % plots with droppings	Inventory method
1973	N/A	N/A	N/A	N/A	N/A
1974	N/A	N/A	N/A	N/A	N/A
1975	N/A	N/A	N/A	N/A	N/A
1976	N/A	N/A	N/A	N/A	N/A
1977	0.137	10.3	0.890	30.6	Old
1978	0.221	14.7	2.840	40.3	Old
1979	0.234	16.00	1.846	31.7	Old
1980	0.199	12.7	1.099	16.0	Old
1981	0.202	13.9	0.689	14.1	Old
1982	0.314	20.9	1.551	24.1	Old
1983	0.521	27.4	1.575	25.0	Old
1984	0.438	23.5	3.015	41.8	Old
1985	0.356	24.8	5.332	58.6	Old
1986	0.309	20.1	3.761	55.8	Old
1987	0.215	12.7	3.100	40.8	Old
1988	0.266	18.5	5.407	63.2	Old
1989	0.365	21.5	4.693	48.1	Old
1990	0.313	17.1	2.003	34.0	Old
1991	0.344	24.3	0.367	25.1	Old
1992	0.281	22.9	0.978	15.6	Old
1993	0.295	24.2	0.651	9.8	Old
1994	0.16	12.00	0.540	8.0	Old
1995	0.37	24.6	0.640	10.2	Old
1996	0.327	23.8	0.565	9.6	Old
1997	0.123	10.1	0.575	7.1	New
1998	0.165	13.5	0.374	8.1	New
1999	0.161	12.2	0.992	11.2	New
2000	0.106	8.8	0.752	8.4	New
2001	0.115	8.4	0.482	5.6	New
2002	0.133	9.5	0.718	9.5	New
2003	0.118	8.7	1.060	15.9	New
2004	0.122	8.9	1.220	17.4	New

2005	0.106	8.2	0.660	10.9	New
2006	0.095	7.5	0.859	10.8	New
2007	0.053	4.2	0.919	9.9	New
2008	0.076	5.5	0.691	7.7	New
2009	0.100	7.9	0.832	9.4	New
2010	0.055	4.3	0.624	6.7	New
2011	0.049	3.6	0.563	8.8	New
2012	0.032	3.2	0.576	5.6	New
2013	0.035	2.8	0.418	5.9	New
2014	0.023	2.1	0.261	3.3	New
2015	0.055	4.2	0.333	4.1	New
2016	0.033	2.2	0.201	2.0	New
2017	0.068	2.8	0.096	1.7	New
2018	0.037	2.4	0.246	2.2	New
2019	0.073	3.5	0.200	1.7	New
2020	0.063	5.1	0.446	3.1	New
2021	0.058	3.8	0.227	2.0	New
2022	0.074	4.6	0.232	2.6	New
2023	0.064	2.3	0.142	2.4	New
2024	0.052	3.2	0.049	1.0	New

Year	Sarcoptic mange	Winter harshness	Snow depth yearly mean	Winter season average degree
1973	0	11.61	0.174	1.33
1974	0	18.91	0.0577	-0.359
1975	0	16.28	0.108	0.634
1976	0	10.99	0.136	-1.18
1977	0	92.01	0.557	-0.969
1978	0	47.06	0.278	-0.978
1979	0	45.68	0.276	-1.78
1980	0	36.59	0.260	-1.13
1981	0	22.76	0.193	-1.11
1982	0	77.8	0.451	-1.42
1983	1	18.59	0.0739	1.00
1984	1	48.9	0.136	0.0393
1985	1	43.36	0.141	-0.874
1986	1	52.5	0.140	-1.95
1987	1	46.22	0.120	-1.37
1988	1	33.8	0.113	0.844
1989	1	10.46	0.0136	1.16
1990	0	5.49	0.0124	1.91
1991	0	19.98	0.0520	1.34
1992	0	4.04	0.0150	1.90
1993	0	5.84	0.0269	1.01
1994	0	47.34	0.120	0.0206
1995	0	26.38	0.0748	1.67
1996	0	14.46	0.0456	-0.382
1997	0	8.01	0.0272	1.34
1998	0	13.14	0.0539	1.19
1999	0	17.84	0.0621	1.65
2000	0	10.75	0.0646	2.56
2001	0	12.55	0.135	1.78
2002	0	17.08	0.175	0.827
2003	0	26.2	0.122	0.0432
2004	0	25.56	0.223	1.30
2005	0	15.83	0.118	1.22

2006	0	49.37	0.359	1.72
2007	0	13.8	0.123	2.18
2008	0	8.53	0.0937	2.14
2009	0	28.99	0.225	1.45
2010	0	54.58	0.259	0.488
2011	0	64.41	0.186	0.633
2012	0	14.26	0.0570	1.78
2013	0	39.72	0.0976	0.714
2014	0	13.2	0.0406	2.87
2015	0	19.5	0.0624	2.07
2016	0	7.56	0.0331	2.08
2017	0	13.28	0.0489	1.39
2018	0	44.62	0.141	1.45
2019	0	33.26	0.0946	1.71
2020	0	2.86	0.00402	2.72
2021	0	14.31	0.0419	2.36
2022	0	9.74	0.0335	1.62
2023	0	13.5	0.0468	1.49
2024	0	42.51	0.119	1.20

Publishing and archiving

Approved students’ theses at SLU can be published online. As a student you own the copyright to your work and in such cases, you need to approve the publication. In connection with your approval of publication, SLU will process your personal data (name) to make the work searchable on the internet. You can revoke your consent at any time by contacting the library.

Even if you choose not to publish the work or if you revoke your approval, the thesis will be archived digitally according to archive legislation.

You will find links to SLU's publication agreement and SLU's processing of personal data and your rights on this page:

- https://libanswers.slu.se/en/faq/228318

☒ YES, I, Emelie Sabrie, have read and agree to the agreement for publication and the personal data processing that takes place in connection with this