BACHELOR THESIS

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Does the wolf (Canis lupus) affect presence of the red fox (Vulpes vulpes) in Sweden?

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Sammanfattning

Vargen (*Canis lupus*) har ökat stadigt i Sverige under de senaste decennierna. Vargens återkomst och dess påverkan på det svenska djurlivet studeras idag i stor utsträckning, och frågor har uppstått om vargen som toppredator kan komma att orsaka trofiska kaskader i ekosystemet, vilket har observerats i nationalparker i USA. Rödräven (*Vulpes vulpes*) har i Sverige visat sig dra stor nytta utav vargens återkomst genom den ökade mängden kadaver som vargen lämnar, vilket är en särskilt viktig födokälla under våren. Syftet med denna studie var att undersöka om närvaro av varg påverkar förekomst av rödräv. Rävspår räknades i 182 vilttrianglar i Örebro och Värmlands län under åren 2001-2003. Vilttrianglarna klassificerades med avseende på mängd jordbruksmark, avstånd till vargrevir och ålder på vargrevir. Effekt av varg på rävförekomst analyserades genom att jämföra rävspår med distans till vargrevir och hur länge det funnits varg i området samt rävspår i relation till mängd jordbruksmark. Studien kunde inte påvisa någon effekt av vargförekomst på räv. Resultaten indikerar på att habitatet var nyckelfaktorn för rävförekomst istället för närvaro av varg. I och med att vargstammen ökar stadigt i Sverige är det dock av intresse med fortsatta studier i ämnet då vargen kan komma att spela en större roll i ekosystemet i framtiden.

Abstract

The wolf (*Canis lupus*) has made a profound comeback in Sweden the last decades. The return of the wolf and its impact on the Swedish wildlife is the object of many studies today, and questions have arisen whether the wolf as an apex predator will cause trophic cascades throughout the ecosystem, as has been observed in USA. The red fox (*Vulpes vulpes*) has in Sweden been found to take advantage of the return of the wolf through the increase of carcass residues, which is an important food source during the spring. The aim of this study was to examine the wolf's impact on the red fox in Sweden and whether presence of wolf affects occurrence of the red fox. 182 wildlife triangles were used to census fox tracks during the years of 2001- 2003 in the counties of Örebro and Värmland, south-central Sweden. Data on amount arable and pasture land, distance to wolf territory and age of territory was also appointed the triangles. By relating number of fox tracks to distances to and ages of wolf territories, possible correlations between wolf and fox occurrence were analyzed. The results could not show any correlation between wolf presence and occurrence of red fox. Instead, the habitat was found to be the key factor affecting fox occurrence. However, as the wolf population is steadily increasing in Sweden, further studies on the impact of wolf seems important as the wolf could come to have a more prominent role in the ecosystem in the future.

Contents

1. Introduction

The wolf (*Canis lupus*) is steadily increasing in Sweden after being close to extinction for over a century (Wabakken et al., 2001, Svensson et al., 2013). When the wolf became a protected species in Sweden in 1966, there most likely only remained 10 individuals in the country and no reproduction was recorded for a longer period (Wabakken et al., 2001). The original Swedish population was by then considered to be functionally extinct. In 1983, a reproduction of a wolf pair with eastern origin was recorded in the Nyskoga territory in northern Värmland (Wabakken et al., 2001). New puppies were born every year in this area from 1983-1990 (excluding 1986) (Wabakken et al., 2001).But it was not until the 1990's that the real turning point occurred and the wolf population growth really took off. In 1991, reproductions were for the first time since the 1950's documented in two territories, Värmland (Nyskoga) and in Gillhov in Jämtland, thanks to an immigrant wolf from the East (Aronsson & Sand, 2004). This would come to greatly increase the population growth rate. New territories with wolf pairs has thereafter been documented for every year (Wabakken et al., 2001), and the Scandinavian wolf population has now grown to about 380 individuals and 38 reproductions in the winter of 2012/13 (Svensson et al., 2013).

The wolf is considered an apex predator, being at the top of the food chain with an essential role in the trophic dynamics, strongly affecting the ecosystems they live in (Ritchie & Johnson, 2009). The role of the wolf as an apex predator has been the focus of several recent studies and the results indicates the wolf as a keystone species that contributes to the wealth of numerous other species (Ripple et al., 2014). The return of the wolf in Sweden can affect the ecosystem and many species both directly and indirectly (Wikenros, 2011).

The wolf plays an important part in providing several other species with food through the carcasses of their prey (Wilmers et al., 2003). Previous studies on the impact of wolves on other animals indicate that the wolf has a positive impact on scavengers such as the red fox (*Vulpes vulpes*), common raven (*Corvus corax*), marten (*Martes martes*) and goshawk (*Accipiter gentilis*) (Selva et al., 2005, van Dijk et al., 2008a, Wikenros, et al., 2013,). The wolf may also affect prey behavior in the sense that increased predation induces a more advanced anti-predator behavior to the wolf among the prey species (Berger et al., 2001). As an apex predator, the wolf has an important role in the ecosystem, and a population increase or decrease can result in consequences all along the food chain through a "trophic cascade" (Sergio et al., 2008). The wolf is often associated with the trophic cascade of its ability to regulate herbivores, reducing pressure on the vegetation, which in turn may favor the smaller animals and birds that require denser vegetation for food and shelter (Sergio et al., 2008, Ripple & Beschta, 2012, Callan et al., 2013). The wolf can also play an essential role in the dynamics of mesopredators and their prey. A mesopredator, often a generalist, occupies the trophic positions below the apex predators (Ritchie & Johnson, 2009). The term "mesopredator release" describes the hypothesis of an apex predators' indirect impact on another trophic level. A reduction of mesopredators through an increase of apex predators, such as the wolf, could result in an increase of the mesopredator's prey (Elmhagen & Rushton, 2007). In absence of apex predators, the mesopredator can reach high densities, which can negatively affect their prey (Ripple et al., 2013). The wolf can hence have a positive indirect impact on another trophic level, the mesopredator's prey (Crooks & Soule, 1999).

1.1 The wolf and the fox
The red fox is a mesopredator species likely to be affected both positively as well as negatively by the return of the wolf. The wolf may pose a threat to foxes by so-called "intraguild

predation", where the wolf as the larger-sized predator can kill the red fox because it constitutes some competition (Thompson et al., 2007). This could affect the movement patterns of the red fox to avoid the wolf territories (Ripple et al., 2013). Although the red fox in that sense may be negatively affected by the wolf's return from an increased predation risk, the fox could also benefit from the carcass residues wolves leave behind (Wikenros et al., 2013). The wolf has increased the carrion biomass available for scavengers during the critical times in the spring (van Dijk et al.,2008a, Koskela et al., 2013). However, the return of the wolf in Sweden has not led to more food for the scavengers such as the red fox. The wolf predation has namely reduced the scavengers' primary food sources, moose dead of natural causes and remains after hunter harvest of moose. Hunters decrease harvest of moose within wolf territories to compensate for the wolf-killed moose and fewer moose die of natural causes due to compensatory wolf predation (Wikenros, 2011). Nevertheless, food availability for scavengers in the form of wolf-killed moose is more evenly distributed over the year with more supply during the critical period in the late winter and early spring, as opposite to human seasonal hunting (Wikenros et al., 2013). In the winter, it is difficult to find other food sources such as rodents that become more inaccessible and decline during this period (Bartoń & Zalewski, 2007), which means that the scavengers can benefit a lot from presence of wolves (Wikenros et al., 2013). Late winter and spring are thus the period when scavenging species' consumption of carrion remains from wolf-killed moose are highest (Jędrzejewski & Jędrzejewska, 1992). Previous studies have demonstrated that the red fox is the most frequent scavenger to visit wolf-killed moose carcasses and that the red fox can follow the wolves for guidance to the prey (Wikenros et al., 2013). In addition, the fox has been showed to eat more carrion in forested habitats, where presence of rodents is low but wolves higher. This shows on the importance of the wolf supplying scavengers as the fox when the fox's main food sources are scarce (Kidawa & Kowalczyk, 2011).

The red fox is a generalist with a wide food choice, and in addition to carrion it eats mostly rodents and small to medium-sized mammals, but also insects and berries (Gorman, 2009). The wolf is not as wide in its food preference as the fox, preferring mostly larger ungulates such as the moose, and occasionally roe deer (Sand et al., 2008). Thus, there is no major competition between wolf and fox over prey (Bassi et al., 2011). In some areas, however, the wolf can eat smaller mammals such as hare and rodents (Weimer, 2009), which could lead to a minor direct food concurrence with the red fox. The red fox population suffered a great reduction during the 1970-80's due to a breakout of fox scabies but is now believed to be restored to its former size, about 150 000 foxes (Svenska Jägareförbundet, 2012). The density of foxes can vary depending on type of landscape and is denser in rich biotopes (Lindström, 2001), such as open farmland, arable fields and pasture areas (Elmhagen & Rushton, 2007). There are often more food available for the fox in these habitats, such as voles, than in the forest. The fox density can thereby vary from 0.2-0.4 foxes per km^2 (forest landscape, mid-Sweden) to 0.8 (pasture landscape, southern Sweden) (Lindström, 2011). As one of the fox's main food sources is voles, the fox population can fluctuate a lot due to a changing population of voles, known as vole cycles (Elmhagen et al., 2011). During peak vole years, which comes with an interval of 3-4 years, the vole population increases, enhancing the food availability for the fox. The improved living conditions due to an increase of food usually lead to an expansion of the fox population the following year (Lindström, 2001).

1.2 The wolf and mesopredator release
When the fox population declined due to the fox scabies, a distinct increase of its prey was noticed, such as mountain hare (*Lepus timidus*), European hare (*Lepus europaeus*), black grouse (*Tetrao tetrix*) and capercaillie (*Tetrao urogallus)* (Kjellander & Nordström, 2003).

When the fox recovered towards the end of the 1980's, and the wolf population was very low, a decrease of the red fox's prey populations could be observed (Lindström, 2001).

Wolves may play an important role in regulating the fox population and thereby reduce the fox predation on the fox's prey (Miller et al., 2012). It is thereby of great interest to study the dynamics of the wolf as an apex predator and the impact on its' surrounding wildlife, if the red fox will increase or decrease depending on wolf occurrence. The coyote, a North American mesopredator equivalent to the red fox, is in many regions a major threat to vulnerable prey species (Berger & Conner, 2008). In areas with wolves, the pressure on these prey species is reduced due to the wolf regulating the coyote population (Ripple et al., 2013). Studies in Scandinavia have showed that the increased presence of lynx (*Lynx lynx*), an apex predator like the wolf, has led to a decline in the fox population (Helldin et al., 2006), but increase in the occurrence of hare, which is a prey to the fox (Elmhagen et al., 2010).

Most studies about the wolf's role in the ecosystem and its impact on other species have been performed in national parks, such as Yellowstone, USA (Ripple & Beschta, 2012), which differ a lot from the in the Swedish nature and ecosystem, largely affected by hunter harvest, modern forestry and agriculture (Wikenros, 2011). The modern forestry has resulted in a great quantity of food for larger herbivores such as moose, making them not limited by the food supply or predation but instead principally regulated by the human hunting (Andrén et al., 2011). With a rapidly expanding wolf population, it is of great interest to study its effect on other species in the Swedish ecosystem. Today, the wolf is still in the process of re-colonizing Scandinavia and thus has a relatively low demographic impact on their prey populations. However, with an increasing wolf population, the greater the impact will probably be (Gervasi et al., 2012).

1.3 Aim of study

The aim of this study is to investigate the effect of wolf presence on the occurrence of red fox. The hypothesis is that the wolf will mainly benefit the fox due to increased food resources during the critical spring period. Fox density should then increase in wolf territories. The study is interesting in the sense that it can illuminate important species interactions in the ecosystem and the value of biodiversity conservation. Also, as most studies about the wolf's role in the ecosystem have been performed in relatively pristine environments in national parks, a study conducted in the Swedish man-made landscape is of great interest

2. Materials and methods

2.1 Study area

The study area is located in the south-central part of Sweden, in the counties of Örebro and Värmland between ca 58°50'N and 60°N. The area is dominated by boreal forest in the north and agricultural land in the south-southwest. About 74% of the total land area of Värmland and 67% of Örebro is forested (Swedish Statistical Yearbook of Forestry, SSYF, 2007). Both Värmland and Örebro are subjected to intensive forestry with a great amount of forest being younger than 50 years (SSYF, 2007). About 6% of Värmland and 16% of Örebro is covered by agricultural land (SSYF, 2007). The environment is however very diverse with many lakes, rivers and mires. The wolf population has its most dense distribution in Sweden around the study area, and in the winter of 2000/2001 the Scandinavian population consisted of 87-97 wolves, 98-114 wolves in 2001/2002 and in the winter of 2002/2003 of 84-100 wolves (Aronson et al., 2001; Wabakken et al., 2002; 2004). In 2002, the vole population was denser than the previous year, which could have led to an increase of the fox population in 2003 due to a higher reproduction rate (Jansson, G., pers.com.).

2.2 Data collection
The tracking data of foxes was collected in equilateral triangular routes, i.e. wildlife triangles (Lindén et al., 1996), during the years 2001-2003. The triangles were placed at predetermined positions about 10 km apart, though the positions of the triangles could be adjusted due to environmental obstacles such as large agricultural fields, rivers and lakes and animal feeding stations (Figure 1). Each side of the triangle was 4 km long, resulting in a 12 km perimeter. Visible markers were placed along the sides of the triangles and their positions were GPS-registered. Intersecting tracks during the winter of predetermined species of mammals and birds was recorded in 182 wildlife triangles. Fifty-six of the triangles were censused during all three years, 105 during two years and 50 during one year. When censused for more than once, the complete data set was 493 tracking events. Data on wolf occurrence and rough estimates of territory borders are available from annual surveys conducted by the county administrative boards (Wabakken et al., 2001; 2002; 2004).
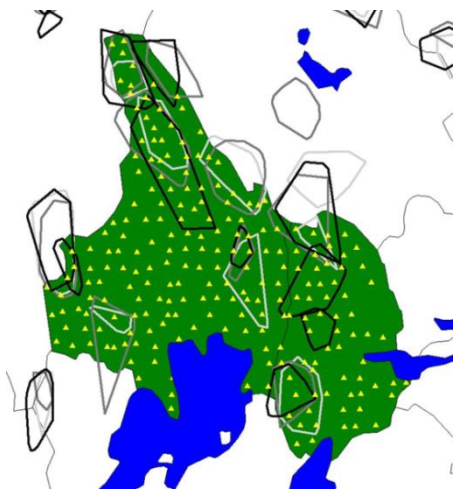

Figure 1: 182 wildlife triangles were placed at predetermined positions in the counties of Örebro and Värmland, south-central Sweden. Fox tracks were censused in the triangles during the winters of 2001-2003. The polygons on the map represent the wolf territories.

2.3 Preparation of data
ArcMap 9.1 (ESRI Corporation, Redlands, CA) was used to assign each triangle environmental properties consisting of the amount of pasture and arable land (Wallgren et al., 2009). The Swedish land cover data (Svenskt marktäcke-data) was used as GIS maps, distributed by National Land Survey (Lantmäteriet) of Sweden. The triangles were imported into the GIS maps with a one 1 km buffer zone and classified by absolute area of arable and pasture land cover. The collected data was compiled into "Triangle-ID", "year of census", "percent proportion of arable" and "pasture land within the triangle" (Wallgren et al., 2009), "number of years since establishment of wolves in territory", "distance to the edge" as well as "distance to center" of wolf territory (km), and number of fox tracks. Distances between wildlife triangles to the edge and center of the wolf territories (Wabakken et al., 2002; 2004) were measured using ArcView 3.0. Fox tracks were divided with the number of 24-hour periods since snowfall, giving the number of tracks per day. Number of years since establishment of wolves in territory was divided into the categories *0*, *1-6* and *19-21* years, (no data of territories with the age of 7-18 years was censused). Distance to edge of wolf territory was divided into the categories *inside* (0 -3.0 km), *uncertain* (3.1-10.0 km) and *outside* (>10.1 km), based on the average size of a wolf territory (1000 km^2) (Mattisson et al., 2013). Distance to center of wolf territory was divided into the categories *inside* (0-18.0 km) (based on the average size of wolf territory), *uncertain* (18.1-23.0 km) (based on the average maximum size of wolf territory

(1700 km^2)) (Mattisson et al., 2013), and *outside* (>23.1 km). Percent arable and pasture land was divided into the categories *little* (0-9%), *intermediate* (10-19%) and *much* (>19%).

For all analyzes except the GLMM, the triangle data from the three years was reduced to only one occasion per triangle, with the majority reduced to the tracking event of 2001. All analyzes were made in SPSS 20.0 (IBM SPSS Inc., Chicago, Illinois, USA).
All analyzes were considered significant at the α-level of <0.05 (95%).

2.4 Statistical analyzes

2.4.1 Wolf territory and fox tracks
A general linear mixed model (GLMM) with a Poisson regression was used to analyze how (1) distance to the center of wolf territory and (2) age of wolf territory affected the number of fox tracks. A Poisson regression is typically used to analyze count data during a fixed time period (UCLA: Statistical Consulting Group).

To analyze the impact of distance to center of wolf territories on the number of fox tracks, the number of fox tracks was entered as the dependent variable and the distance categories as a fixed factor. The habitat factor, proportion of arable/pasture land (categorized), was used as a random factor to account for its known impact on the fox density (Helldin, 2004). Year was entered as a repeated measure and Triangle-ID as the subject.

For the analysis of the age of the wolf territory and its impact on the number of fox tracks, only the triangles placed inside a wolf territory (71 triangles) were analyzed, looking at areas directly affected by wolf presence during different time periods. As a fixed factor, the three age categories of the territories (0, 1-6 and 19-21 years since wolf establishment) were used. The repeated measure, subject, field target and random factor were the same as in the analysis of the impact of distance to center of wolf territory. The odds ratio was used in both analyzes to measure the change in the probability of being present relative to the change in fixed factors.

2.4.2 Comparing abundance of fox tracks before and after establishment of a wolf territory
A comparison was made of the triangles which the first year, 2001, was placed outside a wolf territory but by 2003 was placed inside a territory, meaning a recent establishment of a wolf territory near the triangle had taken place. The triangles which were placed in a territory in 2001, but outside 2003, meaning there was no longer any established presence of wolves, were also analyzed A paired samples t-test was performed for the two analyses to see any eventual increase or decrease in tracks and determine the significant difference between the mean fox tracks during the two different years of 2001 and 2003.

2.4.3 Path analysis
A path analysis was carried out to examine the direct and indirect effect of the different factors; number of fox tracks, proportion of arable/pasture land within triangles and distance to edge of wolf territory. The indirect effect of the distance to wolf territories is the impact on the fox tracks which is mediated through the habitat (amount arable/pasture land). The analysis was performed for each year separately, making three analyses. A linear regression was conducted, which results in a Beta value (standardized coefficient) ranging from -1 (perfect negative correlation) to +1 (perfect positive correlation). The Beta value can be used as a measure of how strong the different factors influence each other, and is therefore useful when comparing the effects (Sundell, 2011). For the first linear regression, distance to edge of wolf territory was entered as the independent value and number of fox tracks as the dependent. This would give a

total effect on the number of fox tracks, including both the impact of distance to territories and amount arable/pasture land (through its indirect effect). A second linear regression was conducted where distance to territories again was entered as the independent value, and amount arable/pasture land as the dependent. The Beta-value of this regression was however only used when calculating the indirect effect. A third, multivariate regression was made with distance to territories and percent arable/pasture land as the independent values and number of fox tracks as dependent, to separate the impacts of distance to wolf territories and habitat. This regression would give the direct effect of both independent values on number of fox tracks. Multiplying the Beta-values of the direct effect of distance to territories on amount arable/pasture land with the effect of amount arable/pasture land on number of fox tracks would give the indirect effect of distance to territories on number of fox tracks (Lleras, 2005). The indirect effect is thereby channeled through the habitat. Dividing the direct and indirect effect of distance to territories on number of fox tracks respectively with the total effect (the Beta-value from the first regression) and multiplying it with 100 gives the proportion of the different effects in percent. The Beta-values of the direct effect of distance to edge of wolf territories on amount arable/pasture land was only calculated for the analysis of the indirect effect, as the distance to wolf territories most likely has no direct effect on the habitat.

3. Results

3.1 GLMM – impact of distance to center and age of wolf territory on number of fox tracks.
No significant effect of the distance to center of wolf territories on the number of fox tracks (Table 1) could be noticed, nor was there any significant effect of age of wolf territories (Table 2).

Table 1: Impact of distance to center of wolf territories on number of fox tracks. The data of fox tracks was collected during the winters of 2001-2003 in wildlife triangles in the counties of Örebro and Värmland in south-central Sweden. Distance to wolf territories was measured in ArcView 3.0.

Model	ß	SE	P	Odds ratio	95% CI for odds ratio	
					Lower	Upper
Outside	0.029	0.121	0.809	1.030	0.811	1.308
Uncertain	0.164	0.169	0.333	1.178	0.845	1.643
Inside	0					

Table 2: Impact of age of wolf territories on number of fox tracks. Data of fox tracks and age of territories was collected during the winters of 2001-2003 in wildlife triangles in the counties of Örebro and Värmland. Only the triangles positioned within wolf territories was used for a comparison of the different age classes.

Model	ß	SE	P	Odds ratio	95% CI for odds ratio	
					Lower	Upper
19-21 years	-0.247	0.223	0.272	0.781	0.501	1.217
1-6 years	-0.231	0.184	0.213	0.794	0.551	1.144
0 years	0					

Comparing number of tracks shows that there were more fox tracks in the triangles which contained much arable/pasture land (Figure 2). The triangles with uncertain position, positioned either inside or possibly outside of a wolf territory, and those for certain outside a territory had

the highest amount of fox tracks, while the triangles positioned inside had the fewest (Figure 3). Triangles with uncertain position At the same time, the triangles positioned inside the wolf territory had the least amount of arable and pasture land, while those outside the wolf territory had the highest. The relationship between habitat and fox tracks also showed a significant bivariate correlation ($p<0.05$), as opposite to distance of center to wolf territory and fox tracks ($p>0.05$).
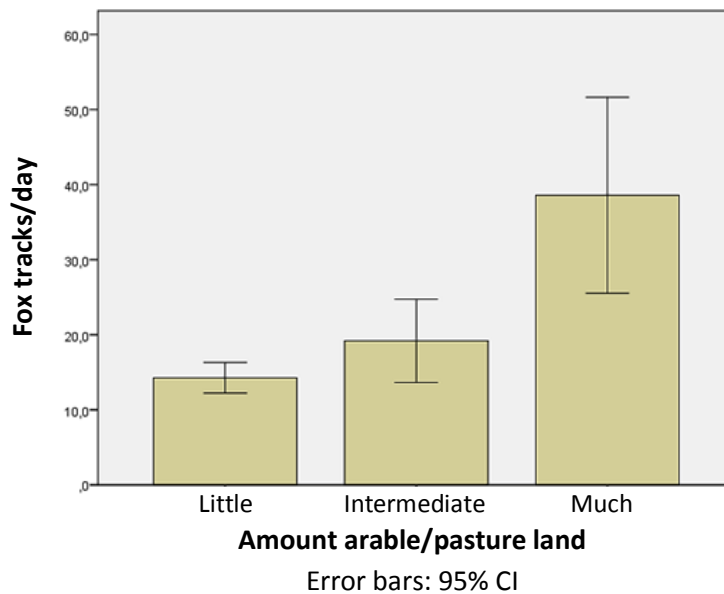

Figure 2: *Number of fox tracks in relation to amount of arable/pasture land in the wildlife triangles. Fox tracks were censused during the winters of 2001-2003 in the counties of Örebro and Värmland, south-central Sweden. Amount of arable and pasture land was assigned each triangle in ArcMap 9.1 by data from the National Land Survey (Lantmäteriet) of Sweden.*
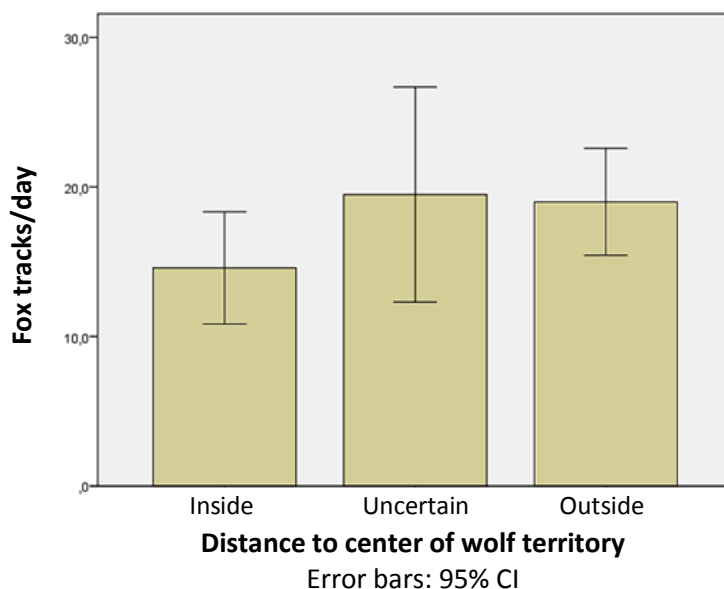

Figure 3: *Number of fox tracks in the wildlife triangles in relation to the triangle's distance to center of a wolf territory. Fox tracks were censused during the winters of 2001-2003 in the counties of Örebro and Värmland, south-central Sweden. Distance to center of wolf territory was measured in ArcView 3.0.*

3.2 Comparing fox tracks before and after establishment of a wolf territory
Only ten wildlife triangles could be used for the analysis. Five triangles were not placed in a wolf territory in 2001, but in 2003 they had become part of one. Four of these triangles had an increase in the number of fox tracks. The paired samples t-test showed a p-value of 0.121 and an increasing mean value from 11.8 fox tracks in 2001 to 24.3 in 2003. Five triangles were placed in a wolf territory in 2001, but outside in 2003. All of the five triangles had a decrease in the number of fox tracks from 2001 to 2003. The paired samples t-test showed a p-value of 0.09 and a decreasing mean value from 23.2 fox tracks in 2001 to 12.1 in 2003.

3.3 Path analysis
The path analyses from the three different years showed that the habitat factor had a greater effect on the number of fox tracks than the distance to edge of wolf territory. In all three years, the direct effect of the distance to the edge of wolf territory gave a lower Beta-value (mean 0.036) than the effect of the habitat factor on the number of fox tracks (mean 0.31) (Figure 4). The higher Beta-value of the direct effect of the habitat on the number of fox tracks means that the correlation between these factors is stronger. The indirect effect, where the impact of distance to edge on fox tracks is channeled through the effect of the habitat, gave a higher Beta value than its direct effect all three years (mean 0.11). Dividing the direct and the indirect effect respectively on the number of fox tracks with their combined sum (the total effect) shows that the indirect effect is greater than the direct (Table 3).
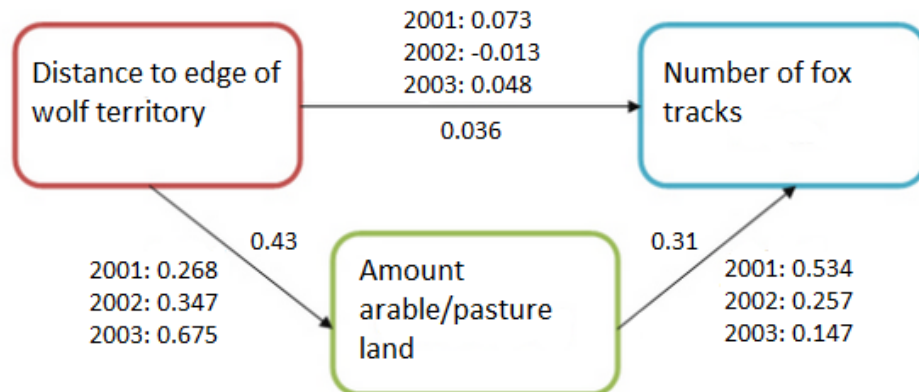

Figure 4: Correlation between distance to edge of wolf territories and arable/pasture land the different years and their mean values. The numbers represent the Beta-values of the direct effects of distance from wolf territories and habitat on the number of fox tracks. There is also an indirect effect where the effect of the distance on number of fox tracks is mediated through the habitat.

Table 3: Indirect and direct effect of distance to edge of wolf territory on the number of fox tracks, calculated through a path analysis. The data was collected in wildlife triangles in south-central Sweden during the winters of 2001-2003.

Year	Indirect effect	Direct effect
2001	66%	34%
2002	117%	-17%
2003	67%	33%
Mean	87%	13%

4. Discussion

4.1 The results
The study could not relate number of fox tracks to the presence of wolves. Thus, even though the red fox can take advantage of the carcass residues that wolves leave behind there was no indication of red foxes being attracted to the wolf territories for improved chances of finding food. The foxes rather tended to keep closer to the habitats with a great amount of arable and pasture land. However, the triangles inside the wolf territories contained the least amount of arable and pasture land. Since there was a significant correlation between the numbers of fox tracks with amount of arable and pasture land, it can be assumed that the habitat may be a more important factor than distance to territory. The path analysis also indicates that the habitat factor has a greater impact on the number of fox tracks than the distance to wolf territory has, as both the direct effect of the habitat and indirect effect is much greater than the direct effect of the distance.

The study did not find any significant effect of the wolf on the number of fox tracks, suggesting that foxes are not affected by whether the territory is young or old but more randomly occurs, or not occurs, in the territories. Notably though, the paired samples t-test showed an increase in fox tracks the year that the triangles was positioned inside a territory compared to when positioned outside. However, the correlations of the two analyses were not significant, which could be the consequence of insufficient data as only 10 out of 182 wildlife triangles could be used in the paired samples t-test.

4.2 The fox and the wolf
Even though the red fox takes advantage of the carcass residues the wolf leave behind (Wikenros et al., 2013), the fox might not have adapted its foraging behavior to search for food closer to the wolf territories. The wolf, still in its way recolonizing the Swedish landscape, can therefore be assumed to not yet have such a persistent impact on the wildlife as the habitat factor (Hedlund, 2008). The human land use today has a more essential significance for the red fox than distance to wolf territory (Mortensen, 2013). Therefore, the fox in Sweden is more dependent on the available food in the agricultural landscape than on carcass residues left by wolves.

Besides preferring habitats with a lot of arable and pasture land (Kurki et al., 1998), the foxes could choose to live further away from the territories to avoid intraguild predation, as has been documented where the fox coexists with lynx in Sweden or coyote in USA (Helldin, 2004, Ripple et al., 2013). Furthermore, studies of the impact of wolves on the wolverine in the Swedish forest landscape have showed that the wolverine greatly benefits from the carcass residues the wolves leave behind (van Dijk et al., 2008a). Even so, the wolverines have been found to not follow the wolves, but instead keeping out of distance to avoid being killed through intraguild predation (van Dijk et al., 2008b).The role of intraguild predation on the fox could thereby become more prominent as the wolf population grows and takes a more dominant role in the Swedish landscape.

4.3 The fox and the landscape
The Swedish landscape is highly shaped by man, with extensive arable fields and forest plantations across the country (Myrdal & Morell, 2011). This has strongly influenced the species composition and life strategies with a need for adaption to the environment (Mortensen, 2013). It has been suggested that the decrease of wolves to a near extinction during the 20th century was a key factor for the red fox populations increase (Elmhagen & Rushton, 2007).

However, the 19th century was characterized by a widespread agricultural expansion and a rapid human population growth in Sweden (Gadd, 2011). This most likely favored the red fox as the chance of finding its favorite food, such as voles, is greater on the fields than in the forest (Kurki et al., 1998). Hence, the agricultural landscape now holds the highest densities of red foxes in Scandinavia (Elmhagen & Rushton, 2007).

The wolf, however, has a lower occurrence in open areas, such as fields, most likely due to a higher human activity (Angelstam et al., 1984, Karlsson et al., 2007). Hence, today the amount of arable and pasture land is relatively low in the wolf territories. Historically, during the decrease of the Swedish wolf population in the 20th century, the decrease was also greatest in the areas where the arable land was increasing the most (Elmhagen, 2007).

4.4 Bottom-up processes
Based on this study, the red fox population in Sweden appears to be foremost regulated by bottom-up processes as the habitat was the key indicator of fox density. In an ecosystem driven by top-down processes, the wolf would as an apex predator control the trophic levels through its ability to suppress mesopredators, and thereby positively affect the mesopredators' prey (Letnic & Dworjanyn, 2011, Brook et al., 2012). The red fox in Sweden however seem to choose habitat based on amount of arable and pasture land, and not being primarily affected by wolf occurrence. The result is compatible with a study by Elmhagen & Rushton (2007) that found that the trophic structure of ecological communities largely depends on the productivity of the landscape. The strength of trophic interactions, such as top-down acting processes and mesopredator release, thereby varies between the ecosystems. In communities foremost affected by bottom-up processes, an increase in apex predators will not have such a significant impact on the mesopredators (Elmhagen & Rushton, 2007)

Reintroducing apex predators is often an argument for mesopredator control and trophic cascades, linking the apex predators to an increase in the mesopredators' prey (Crooks & Soulé, 1999). Since the wolf does not seem to have any strong impact on the red fox in Sweden today, no greater trophic cascade can be expected to occur on the foxes' prey from occurrence of the wolf (Kjellander et al., 2014). Thus, the theory of mesopredator release seems less likely to occur in the dynamics of the wolf, the fox and the fox's prey. However, one thing to have in mind is that there is a probability that through an increase of carcass residues left by wolves, the fox's predation could decrease and the fox's prey thereby increase.

Mesopredator release can, however, be seen in the case of the fox and another apex predator, the lynx. The lynx, which is expanding throughout Sweden, is a more dominant predator on the fox and can have a more significant regulating effect on the fox population size (Helldin et al., 2006). The red fox population has been showed to decrease where lynx occurs, due to intraguild predation (Helldin & Danielsson, 2007). Presence of lynx also leads to an increase in the prey of the fox (Helldin, 2004). In areas where lynx and top-down predation regulation are absent, the fox is foremost affected by the habitat and bottom-up processes (Mortensen et al., 2013). With an increasing wolf population, it is an interesting question whether the wolf could become to have a greater population regulating impact on the red fox and the foxes' prey, in a similar way as the lynx has.

Today however, a broader perspective is needed to maintain biodiversity in anthropogenically altered ecosystems in Sweden, such as the agricultural landscape. Landscape productivity has at the moment a greater impact than mesopredator release on prey population growth (Ritchie &

Johnson, 2009). It is though important to consider both top-down processes and bottom-up processes, as they often interact with each other (Ritchie & Johnson, 2009).

4.5 Conclusion
Today, the wolf in Sweden does not seem to have any essential impact on the red fox population. The key factor for the occurrence of the fox is the habitat, as the fox prioritizes arable and pasture land before closeness to wolves. In comparison with the pristine nature in national parks, the Swedish landscape hosts essential differences for most species, being shaped by and highly associated with human activities (Kjellander et al., 2014). Man has thereby in many ways limited the wolf to the forest landscape, while the fox prefers a habitat with a great amount of arable and pasture land. However, as the wolf recolonizes the Swedish landscape and the population grows in number, they could have an increasing impact on other species (Gervasi et al., 2012). Several studies have showed the importance of carcass residues for the fox during the critical time in spring, when other food sources are scarce (Sidorovich et al., 2005, Selva et al., 2005, Wikenros, 2012). Since the red fox is a frequent visitor at wolf-killed carcasses (Wikenros et al., 2013), the impact of wolves on the red fox's foraging could increase as the wolf population grows. An increased amount of carcass residues could lead to a lower predation rate by the foxes, which favors the foxes' prey. The amount of arable and pasture land in Sweden has been steadily decreasing the last decades (SCB, 2013), in favor of productive woodland (Bråkenhielm, 2000). The future will tell how the mesopredator's foraging in the agricultural land will respond to the new environmental conditions, and if it could lead to foxes staying closer to wolf territories, searching for carcass residues in a wider scale. As the Scandinavian wolf population grows, further research of its impact on the environment and other species is of great interest.

5. References

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