



# Does proactive culling of wolves have an impact on the harvest of moose?

---

Ida Hopia Ivarsson

Degree project in Biology • 30 credits  
Swedish University of Agricultural Sciences, SLU  
Faculty of Forest Sciences • Department of Ecology  
Master of Science in Biology  
Uppsala 2026



# Does proactive culling of wolves have an impact on the harvest of moose?

*Har licensjakt på varg en inverkan på avskjutningen av älg?*

Ida Hopia Ivarsson

**Supervisor:** Camilla Wikenros, Swedish University of Agricultural Sciences, Department of Ecology

**Assistant supervisor:** Håkan Sand, Swedish University of Agricultural Sciences, Department of Ecology

**Assistant supervisor:** Fredrik Widemo, Swedish University of Agricultural Sciences, Department of Wildlife, Fish and Environmental Studies

**Examiner:** Jens Persson, 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

**Programme/education:** Master of Science in Biology

**Course coordinating dept:** Department of Wildlife, Fish, and Environmental Studies

**Place of publication:** Uppsala

**Year of publication:** 2026

**Cover picture:** Left: Wolf track in Jönköping County, Morgan Nilsson  
Right: Harvested female moose, Fredrik Widemo

**Copyright:** All featured images are used with permission from the copyright owner.

**Keywords:** Adaptive management, *Alces alces*, *Canis lupus*, lethal control, moose management goal, sustainable harvest yield, Sweden

**Swedish University of Agricultural Sciences**

Faculty of Forest Sciences

Department of Ecology

SLU Grimsö Wildlife Research Station

## Abstract

Wildlife species are managed on a regional scale in Sweden and moose (*Alces alces*) are managed according to local moose population goals within moose management areas (MMA). The moose is the most important game species for hunters in Sweden. The grey wolf (*Canis lupus*) is a protected species but are managed through proactive culling to limit population size, where the aim is to kill all individuals in selected wolf territories. The aim of this study was to investigate if proactive culling of wolves' result in 1) a decrease in the density of wolves, and 2) an increase in the hunter harvest and the density of moose in Sweden. Harvest statistics of moose (n = 84043) between the hunting seasons 2012/2013 and 2023/2024 from the MMAs (n = 19) within the counties Värmland, Örebro and Västmanland were used. The total harvest per MMA (per km<sup>2</sup>), the proportion of females out of adult harvest, and the proportion of calves out of the total harvest was analysed. The management goals of the moose population (decrease, no-change or increase), the estimated wolf territory density index, moose density before harvest, year, and treatment (culling or not) within the MMA (n=134) were used as explanatory variables. Two different time spans were analysed, a shorter (one year before and one year after culling of wolves) and a longer (three years before and three years after culling of wolves). There was a difference in wolf territory density before culling occurred between MMAs with culling (year 1: wolf index = 0.51) and the control areas (year 1: wolf index = 0.22). Wolf territory density decreased after culling, but the effect was weak (~8 %). For the total moose harvest, the short time span indicated no difference between areas, but for the longer time span, there was a time-lagged effect where in three years after wolf culling, the total harvest increased (14.3 %). None of the included explanatory factors explained variation in the proportion of females in the harvest. The proportion of harvested calves showed that culling of wolves had a negative effect on the harvest of moose, with a weak increase in the proportion harvested calves after the culling occurred. The results from this study is important knowledge for the adaptive management of carnivores and ungulates.

*Keywords: Adaptive management, Alces alces, Canis lupus, lethal control, moose management goal, sustainable harvest yield, Sweden*

# Table of contents

<b>List of tables</b> .....	<b>6</b>
<b>List of figures</b> .....	<b>8</b>
<b>Abbreviations</b> .....	<b>10</b>
<b>1. Introduction</b> .....	<b>11</b>
1.1 Ungulate harvest .....	12
1.2 Carnivore culling .....	12
1.3 Moose harvest in relation to wolf presence .....	13
1.4 Objectives .....	13
<b>2. Method</b> .....	<b>15</b>
2.1 Study area .....	15
2.2 Study species .....	16
2.2.1 Moose .....	16
2.2.2 Wolf .....	16
2.3 Management goals .....	17
2.3.1 Moose .....	17
2.3.2 Wolf .....	18
2.4 Data processing and density calculations .....	19
2.4.1 Goal of moose population .....	19
2.4.2 Moose density .....	19
2.4.3 Moose harvest statistics .....	19
2.4.4 Wolf territory density index .....	19
2.4.5 Proactive culling of wolves .....	20
2.5 Statistical analyses .....	21
2.5.1 Three years before and three years after culling .....	21
2.5.2 Before and after culling .....	22
2.5.3 Overview of wolf culling occurrence .....	22
<b>3. Results</b> .....	<b>24</b>
3.1 Before and after culling .....	25
3.2 Three years before and three years after culling .....	28
<b>4. Discussion</b> .....	<b>34</b>
4.1 Reduced wolf territory density .....	34
4.1.1 Impact on total harvest .....	35
4.2 Moose management goals .....	36
4.3 Future implications and studies .....	36
<b>5. Conclusion</b> .....	<b>38</b>
<b>References</b> .....	<b>39</b>

<b>Popular science summary.....</b>	<b>47</b>
<b>Acknowledgements.....</b>	<b>49</b>
<b>Appendix A .....</b>	<b>50</b>
<b>Appendix B .....</b>	<b>51</b>
<b>Appendix C .....</b>	<b>55</b>
<b>Appendix D .....</b>	<b>56</b>
<b>Appendix E.....</b>	<b>57</b>

# List of tables

Table 1. Prediction of how goal of moose and proactive culling of wolves will affect total harvest. “+” indicates an increase in harvest, “0” indicates no difference in the harvest, and “-” indicates a decrease in the harvest.....	14
Table 2. Number of harvested moose between the hunting year 2012/2013 – 2023/2024 and number of culled wolves between 2015 – 2023 in the counties Värmland, Örebro and Västmanland in south-central Sweden.....	24
Table 3. Summary of the best generalised linear mixed model (GLMM) used to explain the wolf territory density index between 2014/2015 – 2023/2024, explanatory variables included year (before = 1, and after = 2) and treatment (control or culling).....	25
Table 4. Generalized linear mixed model (GLMM) for total harvest density assessing the effect of the interaction between the treatment and year (culling or control, year 1-2) (Y*T), the wolf territory density index (Wolf), the moose management goal (Goal), the moose density (Moose) or between the interactions, the wolf territory density and the management goal (W*G), the treatment and the management goal (T*G), the management goal and the moose density (M*G), or the wolf territory density index and moose density (W*M) on the harvest density of moose (per km <sup>2</sup> ) during 2016/2017 – 2023/2024. The specific management area was included as a random effect. For each model, AICc weights, degrees of freedom (df) and highest-ranked model ( $\Delta AICc$ ) are shown.....	27
Table 5. Summary of the best generalised linear mixed model (GLMM) used to explain the direct effect of the harvest density of moose (km <sup>2</sup> ) in the counties Värmland, Örebro and Västmanland in south-central Sweden between 2016/2017 – 2023/2024. Explanatory variables included treatment (control or culling), the year (year 1-2), the wolf territory density index (Wolf density), the moose density (Moose density) and the moose management goals (increase, unchanged and decrease). The specific MMA were included as a random variable. ....	28
Table 6. Generalized linear mixed model (GLMM) for total harvest density assessing the effect of the interaction between the treatment and year (culling or control, year 1-6)(Y*T), the wolf territory density index (Wolf), the management goal (Goal) or the interaction between the wolf territory density and the management goal (Wolf*Goal), wolf territory density and treatment (W*T) or management goal and treatment (G*T) on harvest density of moose (per km <sup>2</sup> ) during 2012/2013 – 2023/2024 and a generalized mixed-effects model (glmer) for proportions of	

female out of adult harvest and proportion of calves out of total harvest with the same assessments. The specific management area was included as a random effect. For each model, AICc weights, degrees of freedom (df) and highest-ranked model ( $\Delta AICc$ ) are shown..... 31

Table 7. Summary of the best generalised linear mixed model (GLMM) and generalised linear mixed-effects models (glmer) used to explain harvest density of moose ( $km^2$ ), proportion of females out of adult harvest and proportion of calves out of total harvest in the counties Värmland, Örebro and Västmanland in south-central Sweden between 2012/2013 – 2023/2024. Explanatory variables included treatment (Control / Culling), the year (year 1-6), the wolf territory density index (Wolf density) and the moose management goals (increase, unchanged and decrease). The specific MMA were included as a random variable. .... 32

Table 8. Post hoc test for the highest ranked generalised linear mixed model (GLMM) and generalised linear mixed-effects model (glmer) after the culling of wolves (year 3). A pairwise comparison using estimated marginal means and p-values adjusted for multiple comparison using the Tukey method. Average over levels of moose management goal and the wolf territory density index. .... 33

# List of figures

Figure 1. Map of Sweden, the study area (counties Värmland, Örebro and Västmanland) and moose management areas with identification number (n = 19), where harvest of moose were conducted during the hunting season of 2012/2013-2023/2024. ....	15
Figure 2. Wolf territory density index visualised for the monitoring season 2017/2018 in Scandinavia. The study area is shown in green colours (counties Värmland, Örebro and Västmanland) and wolf territory density (calculated for all monitoring seasons during 2012/2013 – 2023/2024). Wolf territory density was calculated by using an 18 km buffer from the annual wolf territory centre. The parabolic gradient shows probability of used territory, the centre (high = 1) to 18 km (low = 0). ....	20
Figure 3. Overview of wolf culling occurrences for the total moose harvest (km <sup>2</sup> ) between 2012/2013 – 2023/2024 in the counties Värmland, Örebro and Västmanland in south-central Sweden. a) MMAs with culling (turquoise) and control (grey). Black circles indicate when culling occurred within the MMA, red circles show culling in the beginning / end of study period, not analysed. b) Thick lines indicate study period (6 years) with wolf culling at year 3, black circles, and small red circles indicates culling that occurred within the study period but are not analysed. c) Study period one year before and one year after culling where black circles indicate wolf culling analysed, and small red circles indicate culling events that were not analysed. ....	23
Figure 4. Mean moose harvest (km <sup>2</sup> ) in control areas (solid line) and culling areas (dashed line) per MMA between 2012/2013 – 2023/2024 in the counties Värmland, Örebro and Västmanland in south-central Sweden. ....	24
Figure 5. Wolf territory density one year before (year 1) and one year after (year 2) the culling of wolves, between the treatment (control or culling) within the counties Värmland, Örebro and Västmanland in south-central Sweden between 2014/2015 – 2023/2024. ....	25
Figure 6. The direct effect in total harvest of moose per km <sup>2</sup> in the moose management areas (MMA) in Sweden (n=19). In relation to the year for the different treatments (a), the management goal of the moose population (b), the wolf territory density (c) and the moose density per km <sup>2</sup> (d). ....	26
Figure 7. Prediction of total harvest of moose per km <sup>2</sup> in the MMAs in Sweden (n=18) in relation to the year and the treatment (control or culling), dashed lined indicate when the culling occurred (a) and the management goals in relation to the wolf territory density index (b). ....	29

Figure 8. Proportion of harvested calves out of total harvest in the moose management areas (MMA) in Sweden (n=18). In relation to the year of the study for both treatments (control and culling), where the dashed line indicates when the culling occurred (a), the moose population management goal (b) and to the wolf territory density index (c).....30

# Abbreviations

CAB	County Administrative Board ( <i>Länsstyrelsen</i> )
MMA	Moose Management Area ( <i>ÄFO - Älgförvaltningsområde</i> )
SEPA	Swedish Environmental Protection Agency ( <i>Naturvårdsverket</i> )

# 1. Introduction

Human actions have had and will continue to influence the environment (Kalis et al. 2003; Dearing et al. 2006). During the 20<sup>th</sup> century, there were three main factors, caused by humans, that contributed to the decline of wildlife populations (e.g. ungulates and carnivores); overharvesting, loss and fragmentation of habitat, and the introduction of alien species (Saltz & White 2013). Overharvesting became less of a cause to the decline after the control of harvest was improved by legislation (ibid.).

When managing wildlife, originally only game species (wildlife that are legally allowed to be hunted), it was important to ensure that the species would be available for harvest the following year (Leopold 1933 see Chesemore 2024). However, since the 1960s, management has a broader focus, it overlaps with conservation, where all wildlife is included, not only game species (Fryxell et al. 2014; Kaltenborn & Linnell 2022). Wildlife as a source, could be seen both as a benefit (ecosystem services) as well as a cost for society (Gren et al. 2018). Ecosystem services from wildlife are divided into three different classes, regulatory, cultural, and providing, but they can also cause an disservice to humans (Widemo et al. 2019). The benefits often derives from the regulatory, cultural and providing categories e.g. recreational activities, nature experiences, hunting and resources from game (e.g. meat, fur and down) (Widemo et al. 2019). The costs and disservices are usually a result of dealing with damages caused by said wildlife, e.g. disease control, fear and predation (Widemo et al. 2019). Dense wildlife populations can cause damage to other human activities such as agriculture, forestry, livestock farming, reindeer husbandry and traffic safety (SEPA 2022).

Impacts from wildlife can be resolved, while conflicts are more of a challenge (Redpath et al. 2013). When different interests are considered against each other, conflicts can arise between humans regarding the interests of the wildlife. According to Redpath et al. (2013), when trying to manage a conflict the best approach is to have a clear goal, have a mutual understanding of the interests and have a transparency between the stakeholders, policy makers and the academics.

Management involves action aimed to achieve a goal, set by humans. According to Fryxell et al. (2014), there are four different ways to manage an animal population, make it increase, make it decrease, and harvest it for a continuous yield (called *manipulative management*) or leave it alone while keeping an eye on it (called *custodial management*). The same authors states that three aspects are needed for the management, (1) what is the goal, (2) what management option is appropriate for said goal, and (3) what action is best to achieve the goal. Depending on what species it is as well as its populations size, distribution and ecological function, the goal will look different.

Wildlife control is a major component in wildlife management (Saltz & White 2013). It is a tool when managing conflicts in environments that are manipulated by humans (ibid.). Both carnivores and ungulates are hunted (culled or harvested) to limit their population growths, minimising spread of diseases and to protect the livelihood of people (e.g. domestic animal husbandry and forestry).

## 1.1 Ungulate harvest

Ungulates are harvested by humans worldwide and predated by large carnivores, but what *type* of animal selected differ. Carnivores often select prey in proportion to their availability and show a preference for juveniles (easy targets) and sometimes senescent animals (older individuals) (Ginsberg & Milner-Gulland 1993; Barber-Meyer & Mech 2008). Trophy hunters (humans), show a disproportionate selection for adult males while game ranchers prefer hunting individuals that are yearlings to maximise the reproductive rate of the herd (Ginsberg & Milner-Gulland 1993).

The selective harvest of ungulates can have a great effect on the species population depending on the individual selected for harvest (sex and age). Survival of adult females are the main factor affecting the population growth, and in hunted populations they often have a lower harvest mortality compared to other age and sex classes (Solberg et al. 2000). In management, it is preferable to harvest non-lactating females over lactating females, to spare individuals with high reproductive potential (Rughetti et al. 2017).

When a larger proportion of adult males are selected for harvest, the number of available males to mate with can fall below the threshold needed to fertilise the reproductive females within the local population (Ginsberg & Milner-Gulland 1993). If the females have not conceived on their first cycle, it will result in delayed births, reduce the birth synchrony, and affect the development of body mass in calves which could lead to higher mortality rates (Ginsberg & Milner-Gulland 1993; Milner et al. 2007).

## 1.2 Carnivore culling

To increase densities of ungulate populations, it has been suggested to decrease carnivore densities to minimise the predator abundance. In a meta-analysis by Clark & Hebblewhite (2020), the authors found that removal of predators had an increased impact on ungulate populations. The impact was modest, but depending on the size of the populations, a modest increase could have a great effect. Removal of predators did also increase the survival of ungulate calves (Clark & Hebblewhite 2020).

### 1.3 Moose harvest in relation to wolf presence

How the presence of wolves (*Canis lupus*) affects the harvest of moose (*Alces alces*) has previously been studied in Scandinavia. Wikenros et al. (2015) found an instant reduction in the harvest of moose in areas where wolves re-established during the earlier years after the return of wolves to the Scandinavian Peninsula. The authors interpreted the results as the hunters over-compensated for wolf predation reducing their harvest more than the estimated number of moose being killed by wolves. In another study, Wikenros et al. (2020) found that in areas with an average wolf territory density, the harvest of moose was 51% lower (in Sweden), compared with areas without wolves.

In 2024, Wikenros et al., discovered that other factors, such as proportion of young forest and the proportion of agricultural land (an index for roe deer (*Capreolus capreolus*) and brown bear (*Ursus arctos*) density), also had an effect on the harvest yield of moose. The total harvest was positively correlated with the proportion of young forest, and with the proportion of agricultural land (Wikenros et al. 2024). The authors suggested that this effect likely was a result of a higher forage resource for moose in younger forests and that higher roe deer densities redirect wolf predation from moose to roe deer. The areas with a higher proportion of agricultural land also coincide with low brown bear density resulting in low brown bear predation on moose.

The harvest among the different age classes of moose in relation to the presence of wolves has previously been studied. For adult females, Wikenros et al. (2020) found that with an increase in wolf territory density hunters responded with decreasing the proportion of females in harvest (out of adult harvest). The same study also showed there were a reduction in harvest of calves with an increase in wolf territory density, and it was suggested that hunters compensated for wolf predation on calves.

### 1.4 Objectives

Whereas several studies have tested for the impact on wolf territory establishment and density on moose harvest (e.g. Wikenros et al. 2015; 2020; 2024; 2025), the aim of this study was to investigate if proactive culling of wolves' results in 1) a decrease in the density of wolves, and 2) an increase in the harvest and density of moose, on a regional scale (moose management areas) in south-central Sweden.

The following predictions (P) were made.

- P1. After proactive culling of wolves within wolf territories, there should be an:
- a. reduced wolf territory density,
  - b. increased harvest density of moose,
  - c. increased proportion of adult females out of adult harvest,
  - d. increased proportion of calves out of the total harvest.

P2. Depending on the management goal of the target moose population, the harvest will differ according to:

- a. if the goal for the moose population density was to decrease the population size, the harvest should be increasing in areas without wolf culling with an even greater increase in the areas with culling,
- b. if the goal for the moose population density was to stay unchanged, the harvest should be stable in areas without culling and increase in areas after the culling occurred,
- c. if the goal for the moose population density was to increase the population size, the harvest should decrease in areas with wolves but be stable in areas after culling (Table 1).

This study will help to further understand how proactive culling of wolves' impact management goals of an important game species.

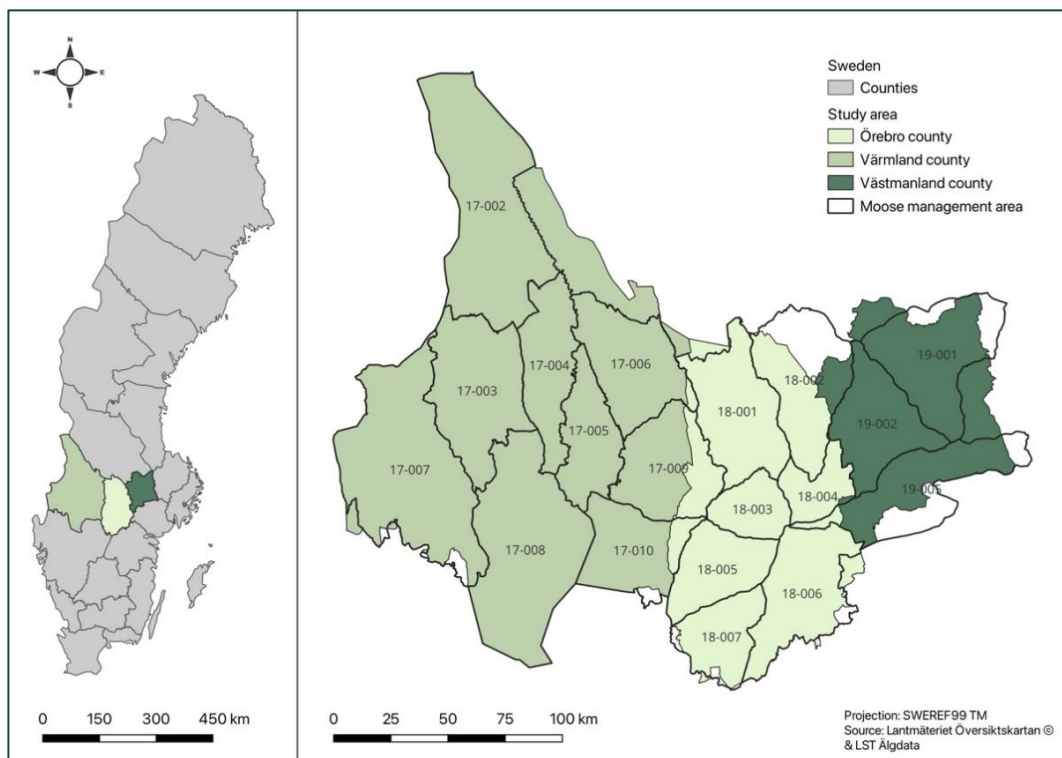
*Table 1. Prediction of how goal of moose and proactive culling of wolves will affect total harvest. "+" indicates an increase in harvest, "0" indicates no difference in the harvest, and "-" indicates a decrease in the harvest.*

Proactive culling of wolves in the MMA	Management goals of moose population density per MMA		
	Decrease	Unchanged	Increase
No	+	0	-
Yes	++	+	0

## 2. Method

### 2.1 Study area

The study area is approximately 30 000 km<sup>2</sup> and includes three counties in south-central Sweden (Värmland, Örebro and Västmanland). In Värmland county, 80 % of the land area consists of boreal forest, the terrain is rocky and there are multiple streams and bodies of water (SCB n.d., Appendix A). Approximately 280 000 inhabitants live in the county, 100 000 of these live in the city of Karlstad. Two highways cross the county. In Örebro county, ~ 75 % of the land area consists of boreal forest while ~ 10 % is agricultural land (SCB n.d., Appendix A). There are approximately 300 000 inhabitants, 130 000 lives in the city of Örebro. Two highways cross the county, and there are a few other major roads. In Västmanland county, ~ 65 % of the land is boreal forest and 20 % is agricultural land (SCB n.d., Appendix A). There are approximately 260 000 inhabitants, 160 000 lives in the city of Västerås. One highway crosses the southern part of the county, and there are some larger roads in the northern parts.



*Figure 1. Map of Sweden, the study area (counties Värmland, Örebro and Västmanland) and moose management areas with identification number ( $n = 19$ ), where harvest of moose were conducted during the hunting season of 2012/2013-2023/2024.*

## 2.2 Study species

### 2.2.1 Moose

The moose is a large, solitary-living ungulate that inhabits boreal forest, *taiga*, and mixed deciduous forest across the Northern Hemisphere. The moose can live up to 25 years, females become reproductive at the age of 2 (at age 15 the fertility usually decreases), while the males become sexually mature around age 7 (Niedzialkowska et al. 2022; SLU Artdatabanken 2026a). The peak of the rut occurs in September, and a single calf or twins are born in May (Niedzialkowska et al. 2022). Their population growth is limited by human harvest and, during the summer large carnivores predate on calves (ibid.). In Sweden, the moose is the most important game species for hunters (Widemo et al. 2025). However, the moose also causes browsing damages to coniferous trees, mainly Scots pine (*Pinus sylvestris*) which causes economic damage to the forestry industry (Widemo et al. 2019).

During the 18<sup>th</sup> century, the moose were rather uncommon in Sweden, but it began to slowly recover during the late 19<sup>th</sup> century due to the introduction of a modern hunting legislation and the extermination of carnivores (Liberg et al. 2010). When the Hunting Act was introduced in 1938, bag limits were enforced and were adjusted after the abundance of moose (Liberg et al. 2010). The Swedish moose population reached its peak during the 1980s, presumably due to several different events that has favoured the moose. These events included the encouragement in harvesting calves instead of adult females, the spread of practicing clear-cutting in the forestry and the replacement to forest plantations where the soil could no longer be used as arable land (Liberg et al. 2010). In 1982, the harvest reached its peak where 183 000 moose were harvested, this number has since declined (Liberg et al. 2010). The latest estimations after the harvest in 2024/2025, where approximately 56 700 moose were harvested, suggests that there is around 240 000 individuals of moose in Sweden (Älgdata n.d.; Widemo & Leonardsson 2025). The continuous decline of the population has caused it to be added to the 2025 red list as “near threatened” (SLU Artdatabanken 2026a).

### 2.2.2 Wolf

In 1966, the wolf was declared a protected species in Sweden (SLU Artdatabanken 2026b). The same year the wolf was declared functionally extinct but has since 1983 started to re-establish in the Scandinavian Peninsula (Wabakken et al. 2001).

Wolves have a rapid growth, an early sexual maturity and a relatively short generation time which allows them to quickly reproduce in an expanding population (Ciucci et al. 2026). The species is adaptable, and as long as there is an adequate food supply and security, it will thrive in lots of different environments (Ciucci et al. 2026). One of these environments are human-modified landscapes, where wolves has shown to adapt successfully (Chapron et al. 2014). Wolves are

cursorial predators, and in the main distribution area in Sweden, the species main prey is moose with roe deer as its second choice (Ciucci et al. 2026; Sand et al. 2016). During winter, a wolf territory will kill a moose every 4 to 5 days, and the kill rate increase to more often (between 2 to 3 days) during summer (Sand et al. 2025). Out of the total number moose killed by wolves, calves make up approximately 90 % during summer and 70 % during winter (Sand et al. 2005; 2006; 2008).

In the Scandinavian wolf population, the social organisation consists of either family groups ( $\geq 3$  animals within a territory), territorial pairs or other territorial or dispersing individuals (Liberg et al. 2012a). The size of their home ranges, varies between 259 and 1,676 km<sup>2</sup> (mean, 1,017 km<sup>2</sup>), where the size increase with latitude and elevation, and decrease with higher densities of roe deer (Mattison et al. 2013).

Threats for the population in Scandinavia includes high inbreeding and low genetic variation following their geographic isolation and low connectivity (Åkesson 2017; Åkesson et al. 2022). Another threat is the poaching (illegal killing), where in a study by Liberg et al. (2012b) suggest that poaching accounted for approximately half of the mortality (51 %), and that it had a significant impact on the recovery of the population. A later study by the same author, suggested similar results, where 189 out of 444 wolves had disappear without known cause (Liberg et al. 2020).

According to the monitoring in 2012/2013, the Scandinavian wolf population had approximately  $380 \pm 30$  individuals (Wabakken et al. 2013). The monitoring in 2023/2024, resulted in approximately 440 wolves in the population, 375 in Sweden and 65 in Norway (Wabakken et al. 2024).

## 2.3 Management goals

### 2.3.1 Moose

After a parliamentary decision in 2010, a new management system of the Swedish moose population was introduced in January 2012, resulting in the establishment of areas called moose management areas (hereafter MMA). The MMAs should mainly include a delimited moose population that is separated by natural or man-made barriers and be able to exceed county borders if necessary (NFS 2011:7). The MMA is managed by a moose management group consisting of three landowners and three hunter representatives, appointed by the County Administrative Board (hereafter CAB). The group shall prepare a 3-year management plan for the area, decide if the population should increase, stay the same or decline, and the plan must be approved by the CAB. If the circumstances change within the MMA (e.g. establishment of a wolf territory), the plan can be revised. Within the MMA, there is also smaller moose management units, licensed areas and unregistered land. For further details see Wikenros et al. (2020).

The goal with the management is to have a viable moose population (high reproduction rates, high calf weights and diseases without any significant impact) and have a balance between browsing damages in forestry and to have an adaptable harvest of moose (SEPA 2018).

### 2.3.2 Wolf

In 2009, the Swedish parliament agreed on the government proposal regarding the motion “*En ny rovdjursförvaltning*”, translated to “*A new predator management policy*” (SEPA 2010). The goal with the motion was that all predator species should be kept at their favourable conservation status (FSC) in accordance with *The Habitats Directive* (Council Directive 92/43/EEC), while taking into account the husbandry of domestic animals and socioeconomic factors (SEPA 2016). It was decided that the growth rate of the wolf population would temporarily be limited and regulated through the help of proactive- and protective culling. In 2010, the first licensed hunt was granted. In 2014, SEPA introduced a new fundamental regulation, NFS 2014:24, stating the following (translated version):

“4 § The County Administrative Board’s decision on proactive culling of wolves shall stipulate **where within the county** the cull may be conducted. Culling of wolves may **not be conducted in territories where genetically important wolves are known** to be established (NFS 2014:24).

In 2015, the hunt shifted to use proactive culling (hereafter culling) within specific territories instead of a specific number of individuals within the country (Appendix B). The annual quota is decided by the Swedish Environmental Protection Agency (SEPA) and is divided among the affected CABs in the three carnivore management areas, northern, central and southern Sweden. If the decision about the culling is not appealed, the hunt usually occurs between 2 January – 15 February (SEPA 2026).

The wolf population must not fall below its minimum viable population (MVP) that is decided, at least once every five years, for each carnivore management area (SEPA 2025a). With the decision of the MVP, it is important to maintain the genetic variation within the population, and for that immigrants are necessary (SEPA 2016).

The goal of the management of wolves is to have a viable population within its area of distribution, prevent damages on livestock and domestic animals but also to take socioeconomic factors into account (e.g. minimise conflict in rural areas and among hunters involved in the moose hunt) (SEPA 2016).

## 2.4 Data processing and density calculations

The data used for this study derives from the hunting seasons between 2012/2013 – 2023/2024.

### 2.4.1 Goal of moose population

The goal of the moose management, in the form of moose management plans regarding all the MMAs per county, are provided by the respective county administrative board. Each plan had a decision regarding the local moose population, if it should decrease, be unchanged or increase over the next three years. If a plan was revised, the new goal was used in the analyses instead of the old decision. If the goal consisted of the combination “be unchanged and decrease”, it was registered as be unchanged (8 occasions, in 5 different MMAs). If a plan had not yet been created (start of study period, 2012, 2013, 2014), the next available goal of the plan was used for the missing years.

### 2.4.2 Moose density

The density of moose (before the harvest), estimated from moose observations (Älgobs) in relation to the regeneration, harvest and other mortality from the previous hunting season, was provided for the different MMAs (between the years 2015-2024, except for one MMA where it was first reported in 2016) (compiled by Widemo & Leonardsson 2025).

### 2.4.3 Moose harvest statistics

Harvest statistics per MMA per year and shapefile maps containing the borders of the MMAs are available at the CABs database “Älgdata” (maps updated 2022-05-10). The MMAs ranges between 600 – 3670 km<sup>2</sup> with average size ( $\pm$  SE) of 1528  $\pm$  49 km<sup>2</sup> (n = 19). The proportion of harvested adult females were calculated out of the adult harvest while proportion of calves were calculated out of total harvest.

### 2.4.4 Wolf territory density index

Centre points from the annual wolf monitoring are available for territorial pairs and family groups (Svensson et al. 2025). The centre points are used to calculate wolf territory density per MMA (wolf index) per year. The calculations are done in QGIS (version 3.34.12-Prizen) and is based on mean territory size from the centre points, 18 km in radius (1,017 km<sup>2</sup>), described in Mattisson et al. (2013) and by following instructions by Loosen et al. (2021) (Figure 2, Appendix C). A value (wolf territory density index) of 0 represents absence of wolves within the MMA, a value of 0.5 indicates an average density of wolves, while  $> 0.5$  indicates that the MMAs has a higher density of wolves (Wikenros et al. 2020). The expected predation rate, at

wolf territory density index 0.5, represents the annual average of 0.12 moose per km<sup>2</sup>, where approximately 80 % are calves (Zimmermann et al. 2015).

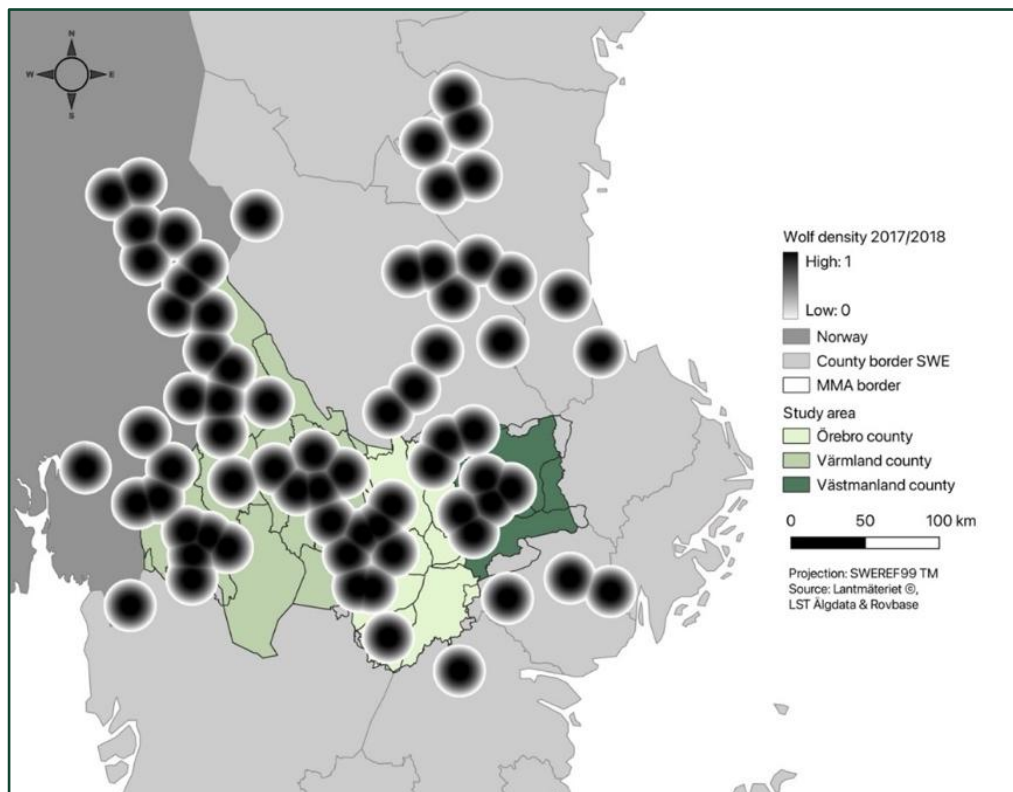


Figure 2. Wolf territory density index visualised for the monitoring season 2017/2018 in Scandinavia. The study area is shown in green colours (counties Värmland, Örebro and Västmanland) and wolf territory density (calculated for all monitoring seasons during 2012/2013 – 2023/2024). Wolf territory density was calculated by using an 18 km buffer from the annual wolf territory centre. The parabolic gradient shows probability of used territory, the centre (high = 1) to 18 km (low = 0).

#### 2.4.5 Proactive culling of wolves

Rovbase is a database that is shared between Sweden and Norway. The website provides information regarding large carnivore monitoring and cause of death to said carnivores (Rovbase n.d.). It provided yearly data for the culled wolves and their location. In order to compile the number of wolves, individual territory belonging, specify sex and age to each culled individual, and get information regarding the allowed quotas for the culling, reports from Rovdata (Rovdata n.d.) and the Swedish Veterinary Agency (SVA) were used (Rovdata reports: Wabakken et al. 2013; 2014; 2016; 2018; 2020; 2022; Svensson et al. 2015; 2017; 2019; 2021; 2023, SVA reports: Söderberg et al. 2010; 2011; Uhlhorn et al. 2013; Åsbrink et al. 2015; Meijer & Ågren 2016; Meijer et al. 2017; SVA rapport 2018; 2021; Ågren & Löwgren 2022; Ågren & Höök 2023; Höök & Ågren 2024; 2025).

## 2.5 Statistical analyses

### 2.5.1 Three years before and three years after culling

#### *Total harvest*

The statistical analyses were conducted in R version 4.5.2 (R Core Team, 2025). A generalized linear mixed model (GLMM) with a gamma-distribution (log link function) from the `glmmTMB` package were used to estimate the impact of the different explanatory variables within the specific area over time (Brooks et al. 2017) (Appendix C). The response variable was the total moose harvest, i.e. the number of moose harvested per km<sup>2</sup> within each MMA. Explanatory variables included: the calculated wolf territory density index (range 0 – 0.788), the local management goal with the moose population (increase, unchanged, decrease), the treatment (MMAs used as; the control area (wolf presence but no culling of wolves) or an area with culling (culling of wolves)), and the year (year 1 – 6, where the culling of wolves occurred between year 3 and 4). Each MMA that had wolf culling (culling of specific wolf territory decided depending on territory centre point overlapping the MMA) (9 MMAs), has a corresponding MMA without culling of wolves as a control (9 MMAs). The year (1-6) and the treatment (control / culling) were always included in the models as an interaction term. The specific MMA was included as a random factor to account for repeated measures. The GLMM with the lowest Akaike Information Criteria (AIC) were selected as the best fitted model for the analysis and the selection was confirmed when using the `model.sel` function from the `MuMIn` package (Bartoń 2026). To further analyse differences between consecutive years and the treatment, a post hoc test with the `emmeans` package was used and the values were adjusted according to the Tukey method (Lenth & Piaskowski 2026).

#### *Proportion adult female out of adult harvest and proportion calves out of total harvest*

A generalized linear mixed-effects model (`glmer`) using the `lme4` package were used for analyses of the proportion of adult females out of adult harvest, and on the proportion of calves out of the total harvest (Bates et al. 2015). To fit the binomial data for the response variable, adult female or calf harvest, the function `cbind` was used in the model (Becker et al. 1988). The explanatory variables were the same as for the first GLMM analysis (year\*treatment, wolf density index and goal of the population) and the specific MMA as the random factor. A post hoc test was done for the model with the lowest AIC value.

## 2.5.2 Before and after culling

### *Total harvest*

To test for the direct impact on the total harvest (one year before and one year after the culling as a treatment), a similar GLMM design was used. The GLMM had a beta-distribution, and the response variable was the total moose harvest. The same explanatory variables were used (wolf territory density, moose management goal and treatment (control / culling)), but with an addition of the moose density prior to the harvest (range 0.470 – 1.566 moose per km<sup>2</sup>) and year (year 1 – 2, where year 1 is prior to the culling and year 2 is after the culling). 12 MMAs had culling of wolves and 7 were used as the control areas. The wolf culling that occurred in 2015 was not included due to missing values in the moose density. One MMA had its first culling in 2024 but was used as a control area for prior years. The culling for 2023 had an uneven ratio between MMAs with culling corresponding to MMAs used as control (7 vs 5).

### *Wolf territory density*

To test if culling reduced the wolf territory density the following monitoring season, a GLMM with beta-distribution was used. The response variable was the wolf territory density index, and the explanatory variables were the year (before = 1 and after = 2) and the treatment (control or culling). The wolf culling that occurred in 2015 and their corresponding control areas were included in this analysis.

## 2.5.3 Overview of wolf culling occurrence

Between the years 2012/2013 – 2023/2024, culling of wolves from a territory occurred 6 times, excluding the cull in 2013 and 2024 (Figure 3a). Three years prior to and after culling occurred for the first time within an MMA was tested in the first analysis (Figure 3b). Three different MMAs that had culling of wolves between year 3 and 4 had additional culling in the 3-year time span after the tested culling (one additional wolf culling during year 5 and two additional during year 6), this was not factored for in the analysis, exclusion of these would reduce the sample size. To analyse a larger dataset of culling occurrences, one year prior to and after the culling of wolves that occurred between 2017-2023 was tested in the second analysis (Figure 3c).

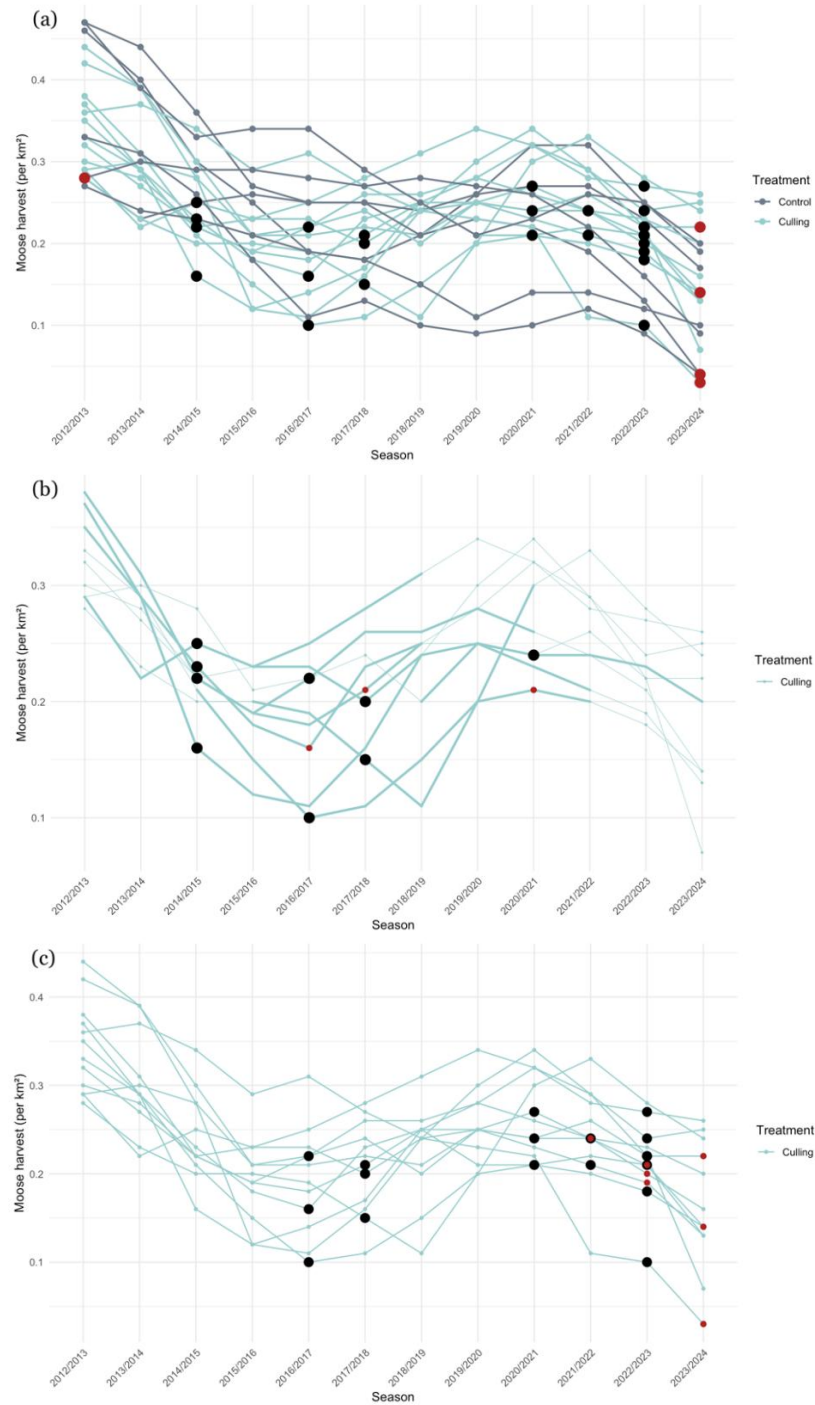


Figure 3. Overview of wolf culling occurrences for the total moose harvest (km<sup>2</sup>) between 2012/2013 – 2023/2024 in the counties Värmland, Örebro and Västmanland in south-central Sweden. a) MMAs with culling (turquoise) and control (grey). Black circles indicate when culling occurred within the MMA, red circles show culling in the beginning / end of study period, not analysed. b) Thick lines indicate study period (6 years) with wolf culling at year 3, black circles, and small red circles indicates culling that occurred within the study period but are not analysed. c) Study period one year before and one year after culling where black circles indicate wolf culling analysed, and small red circles indicate culling events that were not analysed.

### 3. Results

In total 84 043 moose were harvested between 2012/2013 and 2023/2024, and 134 wolves were culled in 31 different territories from 2015 – 2023 (Table 2). The mean of the moose harvest (per km<sup>2</sup>) had a declining trend from 2012/2013 – 2023/2024, and the harvest of moose was higher in all MMAs the first year compared to the last year of the study (Figure 4, Appendix E).

Table 2. Number of harvested moose between the hunting year 2012/2013 – 2023/2024 and number of culled wolves between 2015 – 2023 in the counties Värmland, Örebro and Västmanland in south-central Sweden.

County	Number moose harvested			Number wolf culled	
	Total	Females	Calves	Individuals	Territories
Värmland	50 765	12 116	23 320	79	18
Örebro	21 682	4 896	11 101	43	8
Västmanland	11 596	2 566	6 117	12	5
<b>Total</b>	<b>84 043</b>	<b>19 578</b>	<b>40 538</b>	<b>134</b>	<b>31</b>

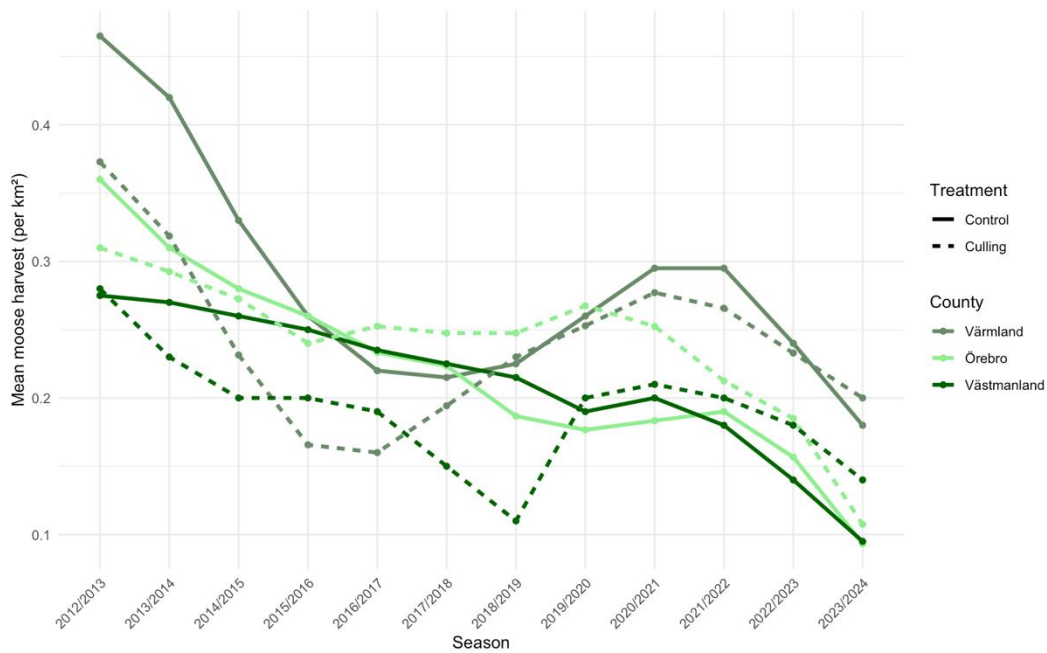


Figure 4. Mean moose harvest (km<sup>2</sup>) in control areas (solid line) and culling areas (dashed line) per MMA between 2012/2013 – 2023/2024 in the counties Värmland, Örebro and Västmanland in south-central Sweden.

### 3.1 Before and after culling

#### *Wolf territory density*

The wolf territory density index differed between the areas (control and culling), where overall the areas with culling had a higher wolf territory density compared to the control areas. For the control areas, the first year resulted in a wolf territory density index of 0.22, with no change in the wolf territory density index the following year (year 2) (Figure 5). For the culling areas, the wolf territory density index had a value of 0.51 before the wolf culling, there was a slight decline (~ 8 %) in the density of wolves after the culling had occurred (wolf-index 0.47) (Figure 5). The decline within the culling areas (before and after) were not significant (estimate = -0.132) (Table 3).

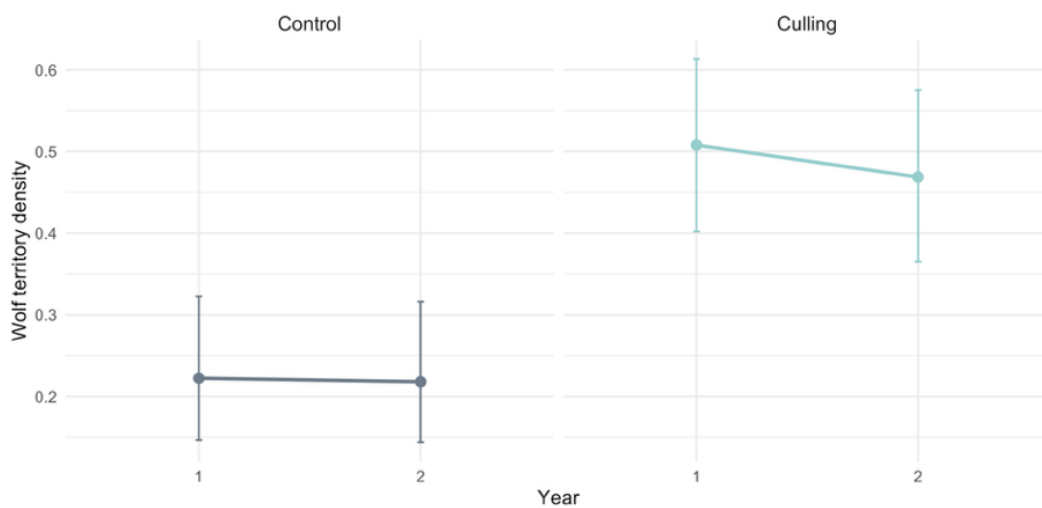


Figure 5. Wolf territory density one year before (year 1) and one year after (year 2) the culling of wolves, between the treatment (control or culling) within the counties Värmland, Örebro and Västmanland in south-central Sweden between 2014/2015 – 2023/2024.

Table 3. Summary of the best generalised linear mixed model (GLMM) used to explain the wolf territory density index between 2014/2015 – 2023/2024, explanatory variables included year (before = 1, and after = 2) and treatment (control or culling).

Response variable	Explanatory variable	$\beta$	SE	z	p-value
Wolf density index	Intercept	-1.252	0.256	-4.888	< 0.001
	Year 2	-0.025	0.207	-0.123	0.902
	Culling	1.284	0.312	4.121	< 0.001
	Year 2: Culling	-0.132	0.271	-0.486	0.627

### Total harvest of moose: direct effect

The highest ranked model when testing the direct effect included the wolf territory density index, the moose management goal, the moose density and the interaction between the treatment and year (Figure 6, Table 4 & 5). The total harvest of moose was lower in both the control areas and the areas with culling the second year (year 2) compared to the first year (year 1) (estimate = -0.156). When the management goal was to increase the moose population, a smaller harvest was conducted compared to when the goal was to let the moose population density be unchanged or to decrease. The total harvest of moose decreased when there was an increase in wolf territory density (estimate = -0.834), and it increased when there was a higher moose density (estimate = 1.333). At minimum moose density (0.470 moose/km<sup>2</sup>), approximately 15 % of the moose were predicted to be harvested while at maximum moose density (1.566 moose/km<sup>2</sup>) approximately 42 % of the moose were predicted to be harvested.

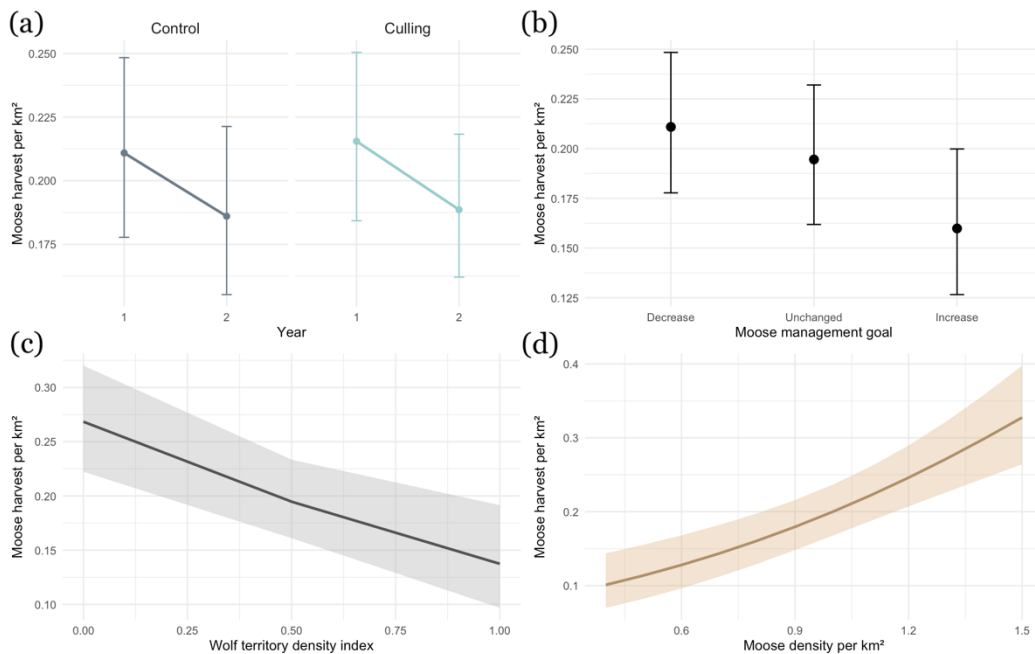


Figure 6. The direct effect in total harvest of moose per km<sup>2</sup> in the moose management areas (MMA) in Sweden (n=19). In relation to the year for the different treatments (a), the management goal of the moose population (b), the wolf territory density (c) and the moose density per km<sup>2</sup> (d).

Table 4. Generalized linear mixed model (GLMM) for total harvest density assessing the effect of the interaction between the treatment and year (culling or control, year 1-2) (Y\*T), the wolf territory density index (Wolf), the moose management goal (Goal), the moose density (Moose) or between the interactions, the wolf territory density and the management goal (W\*G), the treatment and the management goal (T\*G), the management goal and the moose density (M\*G), or the wolf territory density index and moose density (W\*M) on the harvest density of moose (per km<sup>2</sup>) during 2016/2017 – 2023/2024. The specific management area was included as a random effect. For each model, AICc weights, degrees of freedom (df) and highest-ranked model ( $\Delta AICc$ ) are shown.

Response variable	Intercept	Y*T	Wolf	Goal	Moose	W*G	T*G	M*G	W*M	AICc weight	df	$\Delta AICc$
Total harvest density	X	X	X	X	X					0.442	10	0
	X	X		X					X	0.144	11	2.25
	X	X	X	X	X	X				0.105	12	2.87
	X	X			X	X				0.105	12	2.87
	X	X	X					X		0.097	12	3.03
	X	X	X		X					0.065	8	3.84
	X	X	X	X	X		X			0.042	12	4.73
	X	X	X	X						0	9	27.53
	X	X	X							0	7	33.18
	X									0	3	36.53
	X	X					X			0	10	39.87

Table 5. Summary of the best generalised linear mixed model (GLMM) used to explain the direct effect of the harvest density of moose ( $\text{km}^2$ ) in the counties Värmland, Örebro and Västmanland in south-central Sweden between 2016/2017 – 2023/2024. Explanatory variables included treatment (control or culling), the year (year 1-2), the wolf territory density index (Wolf density), the moose density (Moose density) and the moose management goals (increase, unchanged and decrease). The specific MMA were included as a random variable.

Response variable	Explanatory variable	$\beta$	SE	z	p-value
Total harvest	Intercept	-2.402	0.294	-8.169	< 0.001
	Year 2	-0.156	0.077	-2.030	0.042
	Culling	0.027	0.140	0.196	0.845
	Wolf density	-0.834	0.243	-3.439	< 0.001
	Goal: unchanged	-0.101	0.080	-1.273	0.203
	Goal: increase	-0.340	0.113	-3.019	0.003
	Moose density	1.333	0.259	5.141	< 0.001
	Year 2: Culling	-0.011	0.109	-0.098	0.922

## 3.2 Three years before and three years after culling

### *Total harvest*

The highest ranked model included the interaction between year and treatment (culling or control), and the interaction between wolf territory density index and the management goal of the moose population (Figure 7, Table 6 & 7). The predicted harvest of moose was lower in the control areas compared to the areas with wolf culling (year 4, 5 and 6). The total harvest of moose in the area with wolf culling decreased, prior to the cull (year 1-3) but increased after the cull (year 5-6) (Figure 7a).

In MMAs where the management goal was to decrease the moose population, the total moose harvest was not related to the wolf territory density (Figure 7b). In MMAs where the management goal was to let the moose population be unchanged, there was a ~ 31 % decline in total harvest at the maximum wolf territory density (0.788). In MMAs where the management goal was to increase the moose population, there was an ~ 55 % decline in total harvest at maximum wolf territory density.

The post hoc analysis for the total moose harvest indicated that the decline in the control areas after year 3 was significant (year 5 and 6,  $p < 0.05$ ). Within the areas with culling of wolves, there was no statistically significant change after the culling occurred (year 4-6,  $p > 0.5$ ) but there were a 14.3 % increase in moose harvest between year 3 and 6 (Figure 7a, Table 8).

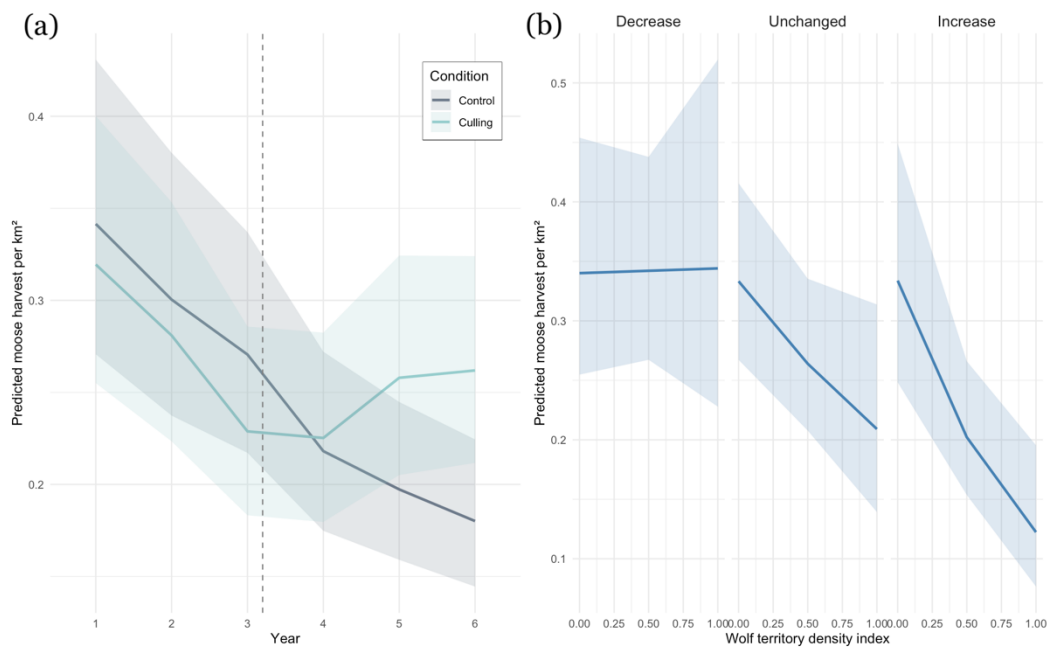


Figure 7. Prediction of total harvest of moose per km<sup>2</sup> in the MMAs in Sweden (n=18) in relation to the year and the treatment (control or culling), dashed lined indicate when the culling occurred (a) and the management goals in relation to the wolf territory density index (b).

#### *Proportion adult females out of adult harvest*

For the proportion of adult females out of the adult harvest, the highest ranked model included only the intercept model (Table 6 and 7). The intercept model had the lowest AIC value and indicated that neither culling of wolves, year, wolf territory density or the management goals had an effect on the proportion of females harvested. Approximately 45 % of the harvested adult moose were adult females.

#### *Proportion calves out of total harvest*

For the proportion of calves harvested out of the total harvest, the highest ranked model included the wolf territory density index, the management goal and the interaction between year and treatment (Figure 8, Table 6 & 7). The proportion of calves harvested was higher in the control areas compared to the areas with culling ( $\beta = -0.27$ ). In the control areas, there was an increase in the proportion harvested calves after year 3. In the areas with wolf culling, there was an increase in the proportion of harvested calves already after the second year (culling of wolves occurred between year 3 and 4). There was no direct change in the proportion of harvested calves in relation to the density of wolves. When the management goal was to reduce the moose population, a lower proportion of calves were harvested as compared to when the goal was to let the moose population density be unchanged

or to increase. In the control areas, approximately 50 % of the total harvest of moose were calves, while in the culling areas 43 % was calves.

In the post hoc analysis for the proportion of calves, the control area had a significant increase after year 3 (year 4, 5 and 6,  $p < 0.05$ ), while the increase for the area with culling was not significant for the same years (all  $p > 0.3$ ) (Table 8).

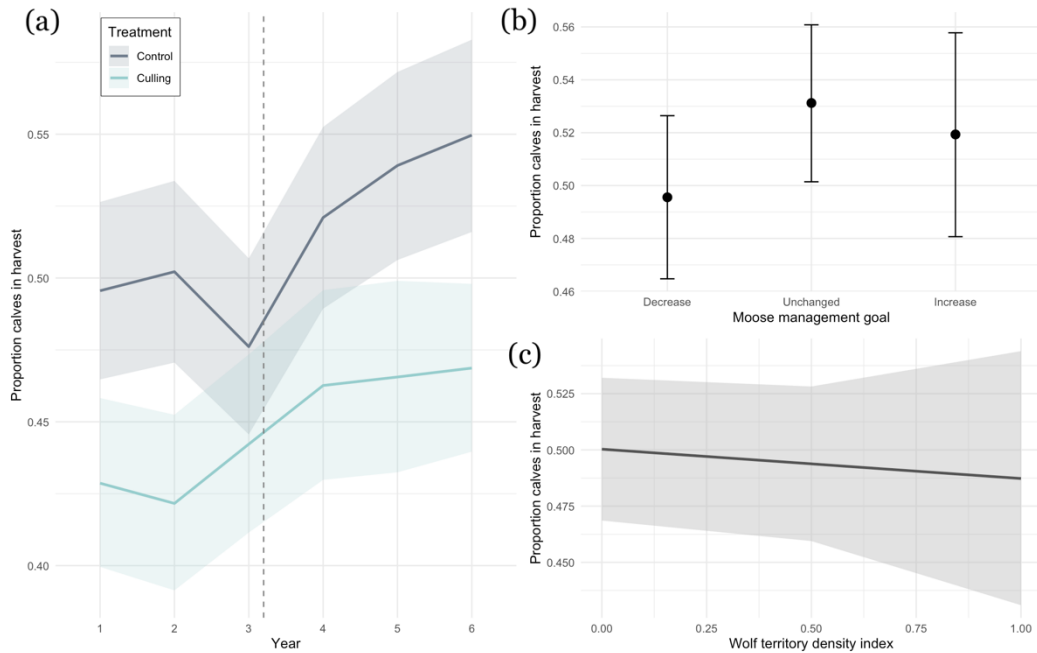


Figure 8. Proportion of harvested calves out of total harvest in the moose management areas (MMA) in Sweden ( $n=18$ ). In relation to the year of the study for both treatments (control and culling), where the dashed line indicates when the culling occurred (a), the moose population management goal (b) and to the wolf territory density index) (c).

Table 6. Generalized linear mixed model (GLMM) for total harvest density assessing the effect of the interaction between the treatment and year (culling or control, year 1-6)(Y\*T), the wolf territory density index (Wolf), the management goal (Goal) or the interaction between the wolf territory density and the management goal (Wolf\*Goal), wolf territory density and treatment (W\*T) or management goal and treatment (G\*T) on harvest density of moose (per km<sup>2</sup>) during 2012/2013 – 2023/2024 and a generalized mixed-effects model (glmer) for proportions of female out of adult harvest and proportion of calves out of total harvest with the same assessments. The specific management area was included as a random effect. For each model, AICc weights, degrees of freedom (df) and highest-ranked model ( $\Delta$ AICc) are shown.

Response variable	Intercept	Y*T	Wolf	Goal	W*G	W*T	G*T	AICc weight	df	$\Delta$ AICc
Total harvest density	X	X			X			0.651	19	0
	X	X			X		X	0.211	21	2.25
	X	X	X	X				0.136	17	3.14
	X	X				X	X	0.002	20	11.39
	X	X	X					0	15	19.87
	X							0	3	53.83
Proportion females out of adult harvest	X							0.986	2	0
	X	X	X	X				0.005	16	10.47
	X	X			X			0.005	18	10.61
	X	X	X					0.003	14	11.77
	X	X	X				X	0.001	18	13.36
	X	X					X	0	19	16.31
Proportion calves out of total harvest	X	X	X	X				0.753	16	0
	X	X			X			0.176	18	2.90
	X	X	X				X	0.055	18	5.22
	X	X				X	X	0.014	19	7.92
	X	X	X					0.001	14	13.19
	X							0	2	60.02

Table 7. Summary of the best generalised linear mixed model (GLMM) and generalised linear mixed-effects models (glmer) used to explain harvest density of moose (km<sup>2</sup>), proportion of females out of adult harvest and proportion of calves out of total harvest in the counties Värmland, Örebro and Västmanland in south-central Sweden between 2012/2013 – 2023/2024. Explanatory variables included treatment (Control / Culling), the year (year 1-6), the wolf territory density index (Wolf density) and the moose management goals (increase, unchanged and decrease). The specific MMA were included as a random variable.

Response variable	Explanatory variable	$\beta$	SE	z	p-value
Total harvest	Intercept	-1.079	0.147	-7.321	< 0.001
	Culling	-0.067	0.157	-0.425	0.671
	Year 2	-0.128	0.864	-1.484	0.138
	Year 3	-0.233	0.087	-2.685	0.007
	Year 4	-0.449	0.087	-5.156	< 0.001
	Year 5	-0.549	0.095	-5.752	< 0.001
	Year 6	-0.640	0.096	-6.663	< 0.001
	Wolf density	0.012	0.262	0.045	0.964
	Goal: Unchanged	-0.020	0.130	-0.156	0.876
	Goal: Increase	-0.019	0.155	-0.120	0.905
	Culling * Year 2	-0.0003	0.123	-0.003	0.998
	Culling * Year 3	-0.101	0.122	-0.829	0.407
	Culling * Year 4	0.099	0.123	0.808	0.419
	Culling * Year 5	0.335	0.128	2.620	0.009
	Culling * Year 6	0.441	0.130	3.398	< 0.001
	Wolf density * Unchanged	-0.478	0.260	-1.837	0.066
Wolf density * Increase	-1.015	0.328	-3.095	0.002	
Proportion female	Intercept	-0.197	0.025	-7.929	< 0.001
Proportion calves	Intercept	0.001	0.065	0.021	0.983
	Culling	-0.270	0.087	-3.092	0.002
	Year 2	0.026	0.047	0.566	0.572
	Year 3	-0.078	0.049	-1.596	0.110
	Year 4	0.102	0.051	1.985	0.047
	Year 5	0.174	0.056	3.139	0.002
	Year 6	0.217	0.058	3.769	< 0.001
	Wolf density	-0.052	0.125	-0.418	0.676
	Goal: Unchanged	0.143	0.034	4.227	< 0.001
	Goal: Increase	0.095	0.061	1.571	0.116
	Culling * Year 2	-0.055	0.066	-0.838	0.402
	Culling * Year 3	0.133	0.069	1.934	0.053
	Culling * Year 4	0.036	0.072	0.500	0.617
	Culling * Year 5	-0.025	0.074	-0.339	0.734
	Culling * Year 6	-0.055	0.075	-0.735	0.462

Table 8. Post hoc test for the highest ranked generalised linear mixed model (GLMM) and generalised linear mixed-effects model (glmer) after the culling of wolves (year 3). A pairwise comparison using estimated marginal means and p-values adjusted for multiple comparison using the Tukey method. Average over levels of moose management goal and the wolf territory density index.

Response variable	Condition	Contrast	$\beta$	SE	z	p-value
Total harvest	Control	Year 3 – Year 4	0.2157	0.0857	2.516	0.1195
		Year 3 – Year 5	0.3158	0.0918	3.439	0.0077
		Year 3 – Year 6	0.4071	0.0931	4.371	0.0002
	Culling	Year 3 – Year 4	0.0158	0.0859	0.184	1.0000
		Year 3 – Year 5	-0.1197	0.0878	-1.364	0.7489
		Year 3 – Year 6	-0.1351	0.0901	-1.499	0.6651
Proportion calf	Control	Year 3 – Year 4	-0.1796	0.0534	-3.361	0.0101
		Year 3 – Year 5	-0.2523	0.0573	-4.406	0.0002
		Year 3 – Year 6	-0.2949	0.0593	-4.976	<0.0001
	Culling	Year 3 – Year 4	-0.0823	0.0542	-1.518	0.6529
		Year 3 – Year 5	-0.0942	0.0545	-1.728	0.5134
		Year 3 – Year 6	-0.1067	0.0537	-1.986	0.3503

## 4. Discussion

Proactive culling of wolves resulted in a decrease in the density of wolves, an increase in the total harvest density of moose and an increase for the proportion of harvested calves out of the total harvest. There was no increase in the proportion of females out of the adult harvest. The harvest did not differ according to the different moose management goals.

### 4.1 Reduced wolf territory density

Culling of wolves did not have a statistically significant impact on the wolf territory density, although there was a slight reduction. This result deviated from the first prediction (P1.a). In a study by Sand et al. (2022), the authors showed that a new wolf territory is likely to re-establish within the previous territory area approximately 1.1 year (range 0 to 11) after the removal or disappearance of the first territory. How quickly the territory would be re-established is dependent on the size of the population as well as how close neighbouring territories are located (Sand et al. 2022). The authors also found that if one of the individuals die (from e.g. culling, natural causes or poaching), a new pair will be present the following monitoring season. It was shown that males are replaced quicker compared to females, since male wolves often disperse for further distances (mean: males 131 km, females 90 km). It could also be possible that the territory would be re-colonised by a new pair of wolves or a previous offspring that would form a pair with a dispersing wolf from a different territory.

The results in this study revealed a difference in the wolf territory density depending on the type of area, if the area have had culling (before culling, in year 1, wolf-index = 0.51) or not (control area, year 1, wolf-index = 0.22). This result is plausible since culling of wolves are mainly carried out in regions where the wolf populations have a higher density, in order to limit the negative socio-economic (e.g. increase moose harvest and reduce depredation) and psychosocial (e.g. fear of living in an area with wolves) impacts caused by wolves on humans (Miljö- och energidepartementet 2015).

The management of wolves are politically and ecologically complex, due to that management strategies and human attitudes are not aligned (Storch et al. 2024). An increased removal of wolves might result in a higher harvest yield of moose, but this needs to be balanced with also having a viable wolf population with favourable conservation status. But it is also of importance to account for the human side of the conflict to understand the public values and not only the biological monitoring (Storch et al. 2024). As Aldo Leopold (1966, see Storch et al. 2024) mentioned: *“The problem of game management is not how we shall handle the deer – the real problem is one of human management. Wildlife management is completely easy;*

*human management difficult*”. In 2025, the reference value of wolves needed to have a minimum viable population (MVP) was reduced to 170 individuals (SEPA 2025b). This reduction seems to favour human interests over the wolves’ ecological function. This reduction of wolves is not yet implemented. According to the European Commission, the reference value of the MVP does not meet the requirements of the Habitat Directive, resulting in them appealing the decision (Le Moine 2025).

#### 4.1.1 Impact on total harvest

In the short time span (before and after wolf culling), the moose harvest decreased from the first year to the second year in both wolf culling and control areas. For the longer time span (three years prior and three years after wolf culling), the moose harvest did increase after the wolf culling, but the increase was not statistically significant. This result did not follow the prediction (P1.b). In a similar study by Miller et al. (2022), the authors studied the efficiency of culling large carnivores to enhance the harvest of moose in Alaska for nearly 40 years. In that study the authors documented a significant negative correlation between the wolf culling and harvest of moose, but they argued that this was due to a temporal coincidence. The study also allowed for a time-lagged effect of 3 years to see if wolf harvest had an impact on the moose harvest, but the impact was not significant (Miller et al. 2022). In this study, there was a general decline in the harvest of moose during the study period (Figure 4). It is possible that the decline in moose harvest could have had an impact on the results, this was tested between the areas (culling and control), but not over time. Widemo & Leonardsson (2025), suggests that hunters opposed official management objectives by trying to reverse the decline in the moose population, since less moose were harvested and observed in 2024 compared to 2012, when the new management system was introduced.

#### *Proportion of adult females out of adult harvest*

For the proportion of adult females out of adult harvest, the intercept model was the highest ranked model, indicating that culling of wolves had no effect on the proportion harvested adult females within three years after the wolf culling had occurred. This was not predicted (P1.c). This result differed from the results in the studies by Wikenros et al. (2020; 2024), but these studies were over a longer duration of time. In these studies, the authors discovered a decrease in the harvested females, and they suggested that this was a result of a compensatory response, since it was believed that hunters wanted to spare the animals with a higher reproductive value. A similar explanation was found in a report by Widemo & Leonardsson (2025), where the authors theorises that hunters harvest less adult female moose, since the females are the most important individuals when it comes to reproduction. In addition, when an adult female moose is together with her calf, it would be

against official *hunting ethics* to shoot the female and not the calf. During the moose hunting season ethical approved hunting is of importance (swe: *jägarmässig avskjutning*) (Svenska Jägareförbundet 2025). The results may also suggest that the management strategy since the “new” regulations in 2012 in Sweden, has been skewed towards the harvest of males.

#### *Proportion of calves out of total harvest*

For the proportion of calves out of the total harvest, there was an increase in harvest regardless the treatment, but the post-hoc test indicated that the change after the third year was only significant in the control and not in the culling areas. The opposite pattern after culling was found in the study by Wikenros et al. (2020), where the authors saw a reduction in harvest of calves with an increase in wolf territory density. The authors suggested that this was due to hunters compensating for predation on calves.

## 4.2 Moose management goals

The results showed that the management goals were not an important factor explaining the variation in neither the total harvest or the composition of the harvest (proportion of females out of adult harvest and the proportion of calves out of total harvest). One explanation could be that the management goals of the moose populations are decided by the individual MMAs, where the MMAs decide how large they want their local moose population to be or to become. The goals are pre-decided for a period of 3 years and has limited possibilities to change within that time unless something drastic happen with the moose population or within the MMA. As moose management plans are made on a three-year basis and wolf culling is decided on a one-year basis (approximately six months before the culling) these management decisions mostly do not coincide in time.

The moose management goal is also decided in relation to the browsing damages caused by moose within the MMAs, where damages on pine should not go above 5 % browsing on young forest (Skogsstyrelsen 2025). A higher density of moose may result in higher browsing damage. In this study, the moose density could only be included in relation to the total harvest for the shorter time span (before and after), and not for the longer time span due to missing data during the earlier years of the study period. Moose density was included in all the highest ranked models (Table 4) and would indeed have been of high interest to include for the longer time span (six years) as well.

## 4.3 Future implications and studies

The carnivores' existence within a human dominated landscape will likely always be questioned. Likewise, how the management of said carnivore or ungulate species

are implemented. According to the Swedish hunting Law, paragraph 4 (SFS 1987:259), the wildlife shall be conserved but also take public and private interests into account. Is it ethically accepted to hunt? Are there other ways to minimise damage to human property without killing wildlife? These questions will probably never be answered with an answer that are accepted by the public and all people of interest, but with more knowledge how the interactions in nature occur and how the different management strategies work, an acceptable answer will get closer.

Roe deer density, brown bear density and the proportion of young forest are factors that previously has been shown to influence the moose harvest (Wikenros et al. 2024) and are important factors to include in potential future studies. It would be interesting to continue the study with the addition of fallow deer- (*Dama dama*), red deer- (*Cervus elaphus*) and wild boar- (*Sus scrofa*) densities, since all three species has increased in large parts of Sweden. These species are also believed to be a part of the wolves' diet in the southern part of the wolf distribution range in Sweden. Their densities could also have an impact on the harvest of moose as wolves for example switch to roe deer instead of moose once the roe deer densities are high enough (Sand et al. 2016).

All the proactive culling of wolves that has occurred in Sweden is well documented and it is possible to expand the study including all the counties where culling has occurred. It would also be interesting to continue the study, to assess the long-term effect of culling of wolves, and to include the status of the individual wolves that were culled in those cases when all individuals in a territory were not killed. Additionally, to include to what extent a culled territory has overlapped with the MMAs and to increase the study period including also the first years with culling (2010 to 2014) when the target was not to remove all individuals per territory.

## 5. Conclusion

The results from this study provides important insight for the adaptive management of ungulates and large carnivores in Sweden. Does proactive culling of wolves have an impact on the harvest of moose? Yes, it does, but the impact was weak. This study shows that proactive culling of wolves has a complex impact on the harvest of moose. This suggests that while wolf culling may contribute to increased moose harvest, it is unlikely to be a decisive management tool on its own.

In relation to current management goals in Sweden, which aim to maintain both a viable moose population and a favourable conservation status for wolves, the results indicate that proactive wolf culling only partially aligns with these objectives. While a reduction in wolf territory density may ease predation pressure on moose, the limited effect observed in this study suggests that such measures may not substantially enhance moose harvest at a broader scale.

Overall, this study emphasizes the complexity of predator-prey management, to effectively balance ecological sustainability with human interests. Further research is necessary to better understand the long-term consequences of wolf management strategies. Such knowledge is essential for evaluating the efficiency of management actions and for achieving the dual goal of sustaining both moose and wolf populations in the Scandinavian peninsula.

# References

- Ågren, E. & Höök, E. (2023). *Licensjakt på varg 2023, resultat från undersökningar på SVA*. (84). Statens veterinärmedicinska anstalt, SVA.
- Ågren, E. & Löwgren, M. (2022). *Licensjakt på varg 2022, resultat från undersökningar på SVA*. (74). Statens veterinärmedicinska anstalt, SVA.
- Åsbrink, J., Malmsten, J. & Ågren, E. (2015). *Licensjakt på varg 2015*. Statens veterinärmedicinska Anstalt, SVA
- Åkesson, M. (2017). *Sammanställning av släkträderna över den skandinaviska vargstammen fram till 2016*.
- Åkesson, M., Flagstad, Ø., Aspi, J., Kojola, I., Liberg, O., Wabakken, P. & Sand, H. (2022). Genetic signature of immigrants and their effect on genetic diversity in the recently established Scandinavian wolf population. *Conservation Genetics*, 23 (2), 359–373. <https://doi.org/10.1007/s10592-021-01423-5>
- Älgdata. (n.d.). Länsstyrelserna. <https://www.algdata.se/>
- Barber-Meyer, S.M. & Mech, L.D. (2008). Factors Influencing Predation on Juvenile Ungulates and Natural Selection Implications. *Wildlife Biology in Practice*, 4 (1), 209-223. Doi:10.2461/wbp.2007.4.2
- Bartoń K (2026). MuMIn: Multi-Model Inference. R package version 1.48.19, <https://CRAN.R-project.org/package=MuMIn>.
- Bates D, Mächler M, Bolker B, Walker S (2015). “Fitting Linear Mixed-Effects Models Using lme4.” *Journal of Statistical Software*, 67(1), 1–48. doi:10.18637/jss.v067.i01.
- Becker RA, Chambers JM, Wilks AR (1988). *The New S Language*. Chapman and Hall/CRC, London. ISBN 053409192X.
- Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017). “glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modelling.” *The R Journal*, 9(2), 378–400. doi:10.32614/RJ-2017-066.
- Chapron, G., Kaczensky, P., Linnell, J.D.C., Von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedó, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfel, M., Wölfel, S., Zimmermann, F., Zlatanova, D.

- & Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, 346 (6216), 1517–1519.  
<https://doi.org/10.1126/science.1257553>
- Chesemore, D.L. (2024). Wildlife management. EBSCO Research.  
<https://www.ebsco.com/research-starters/history/wildlife-management#bibliography> [10-04-2026]
- Ciucci, P., Sand, H., Åkesson, M. & Kusak, J. (2026). Wolf *Canis lupus* Linnaeus, 1758. I: Loy, A. & Ciucci, P. (red.) *Carnivora*. Springer Nature Switzerland. 279–341.  
[https://doi.org/10.1007/978-3-030-44035-0\\_118](https://doi.org/10.1007/978-3-030-44035-0_118)
- Clark, T.J. & Hebblewhite, M. (2020). Predator control may not increase ungulate populations in the future: A formal meta-analysis. *Journal of Applied Ecology*, 58 (4), 812–824. <https://doi.org/10.1111/1365-2664.13810>
- Council Directive 92/43/EEC
- Dearing, J.A., Battarbee, R.W., Dikau, R., Larocque, I. & Oldfield, F. (2006). Human–environment interactions: learning from the past. *Regional Environmental Change*, 6 (1–2), 1–16. <https://doi.org/10.1007/s10113-005-0011-8>
- Fryxell, J.M., Sinclair, A.R.E. & Caughley, G. (2014). *Wildlife Ecology, Conservation, and Management*. 3. edition. John Wiley & Sons, 2014.
- Ginsberg, J.R. & Milner-Gulland, E.J. (1994). Sex-Biased Harvesting and Population Dynamics in Ungulates: Implications for Conservation and Sustainable Use. *Conservation Biology*, 8 (1), 157-166. <https://doi.org/10.1046/j.1523-1739.1994.08010157.x>
- Gren, I.-M., Häggmark-Svensson, T., Elofsson, K. & Engelman, M. (2018). Economics of wildlife management—an overview. *European Journal of Wildlife Research*, 64 (2), 22. <https://doi.org/10.1007/s10344-018-1180-3>
- Höök, E. & Ågren, E. (2024). *Licensjakt på varg 2024, resultat från undersökningar på SVA*. (98). Statens veterinärmedicinska anstalt, SVA.
- Höök, E. & Ågren, E. (2025). *Licensjakt på varg 2025, resultat från undersökning på SVA*. (110). Statens veterinärmedicinska anstalt, SVA.
- Kalis, A.J., Merkt, J. & Wunderlich, J. (2003). Environmental changes during the Holocene climatic optimum in central Europe - human impact and natural causes. *Quaternary Science Reviews*, 22 (1), 33–79. [https://doi.org/10.1016/S0277-3791\(02\)00181-6](https://doi.org/10.1016/S0277-3791(02)00181-6)
- Kaltenborn, B.P. & Linnell, J.D.C. (2022). The Coexistence Potential of Different Wildlife Conservation Frameworks in a Historical Perspective. *Frontiers in Conservation Science*, 2, 711480. <https://doi.org/10.3389/fcosc.2021.711480>
- Le Moine, R. (2025). *Sveriges referensvärde för varg*. (Interpellation 2025/26:188). [https://www.riksdagen.se/sv/dokument-och-lagar/dokument/interpellation/sveriges-referensvarde-for-varg\\_hd10188/](https://www.riksdagen.se/sv/dokument-och-lagar/dokument/interpellation/sveriges-referensvarde-for-varg_hd10188/).
- Lenth R & Piaskowski J (2026). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 2.0.3, <https://rvlenth.github.io/emmeans/>.

- Liberg, O., Aronson, Å., Sand, H., Wabakken, P., Maartmann, E., Svensson, L. & Åkesson, M. (2012a). Monitoring of wolves in Scandinavia. *Hystrix, the Italian Journal of Mammalogy*, 23 (1). <https://doi.org/10.4404/hystrix-23.1-4670>
- Liberg, O., Bergström, R., Kindberg, J., von Essen, H. (2010). Ungulates and their management in Sweden. Apollonio, M., Andersen, R., Putman, R. (eds.). *European Ungulates and their Management in the 21st Century*. Cambridge University Press. 37-70. ISBN: 978-0-521-76061-4.
- Liberg, O., Chapron, G., Wabakken, P., Pedersen, H.C., Hobbs, N.T. & Sand, H. (2012b). Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. *Proceedings of the Royal Society B: Biological Sciences*, 279 (1730), 910–915. <https://doi.org/10.1098/rspb.2011.1275>
- Liberg, O., Suutarinen, J., Åkesson, M., Andrén, H., Wabakken, P., Wikenros, C. & Sand, H. (2020). Poaching-related disappearance rate of wolves in Sweden was positively related to population size and negatively to legal culling. *Biological Conservation*, 243, 108456. <https://doi.org/10.1016/j.biocon.2020.108456>
- Loosen, A.E., Devineau, O., Zimmermann, B., Cromsigt, J.P.G.M., Pfeffer, S.E., Skarpe, C. & Marie Mathisen, K. (2021). Roads, forestry, and wolves interact to drive moose browsing behavior in Scandinavia. *Ecosphere*, 12 (1), e03358. <https://doi.org/10.1002/ecs2.3358>
- Mattisson, J., Sand, H., Wabakken, P., Gervasi, V., Liberg, O., Linnell, J.D.C., Rauset, G.R. & Pedersen, H.C. (2013). Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. *Oecologia*, 173 (3), 813–825. <https://doi.org/10.1007/s00442-013-2668-x>
- Meijer, T. & Ågren, E. (2016). *Licensjakt på varg 2016*. (38). Statens veterinärmedicinska Anstalt, SVA.
- Meijer, T., Uhlhorn, H., Bröjer, C. & Ågren, E. (2017). *Slutrapport Licensjakt på varg 2017*. (39). Statens veterinärmedicinska anstalt.
- Miljö- och energidepartementet (2015). *Uppdrag att utreda gynnsam bevarandestatus för varg*. (Regeringsbeslut M2015/1573/Nm). Regeringskansliet.
- Miller, S.D., Person, D.K. & Bowyer, R.T. (2022). Efficacy of Killing Large Carnivores to Enhance Moose Harvests: New Insights from a Long-Term View. *Diversity*, 14 (11), 939. <https://doi.org/10.3390/d14110939>
- Milner, J.M., Nilsen, E.B. & Andreassen, H.P. (2007). Demographic Side Effects of Selective Hunting in Ungulates and Carnivores. *Conservation Biology*, 21 (1), 36–47. <https://doi.org/10.1111/j.1523-1739.2006.00591.x>
- NFS 2011:7 Naturvårdsverkets författningssamling och allmänna råd m jakt efter älg och kronhjort
- NFS 2014:24 Naturvårdsverkets författningssamling och allmänna råd för länsstyrelsens beslut om licensjakt på varg.

- Niedziałkowska, M., Nuemann, W., Borowik, T., Kołodziej-Sobocińska, M., Malmsten, J., Arnemo, J.M. & Ericsson, G. (2022). Moose *Alces alces* (Linnaeus, 1758). Hackländer, F., Zachos, F.E. (eds.). *Handbook of the mammals of Europe*. Springer Nature Switzerland. 215-245. [https://doi.org/10.1007/978-3-319-65038-8\\_23-1](https://doi.org/10.1007/978-3-319-65038-8_23-1)
- QGIS.org. (2026). QGIS Geographic Information System. QGIS Association. <https://www.qgis.org/>
- R Core Team (2025). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Redpath, S.M., Young, J., Evely, A., Adams, W.M., Sutherland, W.J., Whitehouse, A., Amar, A., Lambert, R.A., Linnell, J.D.C., Watt, A. & Gutiérrez, R.J. (2013). Understanding and managing conservation conflicts. *Trends in Ecology & Evolution*, 28 (2), 100–109. <https://doi.org/10.1016/j.tree.2012.08.021>
- Rovbase. (n.d.). Open access database of Scandinavian large carnivore monitoring. <https://www.rovbase.se>
- Rovdata. (n.d.). Norsk institutt for naturforskning (NINA). <https://www.rovdata.no>
- Rughetti, M., Festa-Bianchet, M., Côte, S.D. & Hamel, S. (2017). Ecological and evolutionary effects of selective harvest of non-lactating female ungulates. *Journal of Applied Ecology*, 54 (5), 1571-1580. doi: 10.1111/1365-2664.12863
- Saltz, D. & White, G.C. (2013). Wildlife Management. I: Encyclopedia of Biodiversity. Elsevier. 403–407. <https://doi.org/10.1016/B978-0-12-384719-5.00274-4>
- Sand, H., Eklund, A., Zimmermann, B., Wikenros, C. & Wabakken, P. (2016). Prey Selection of Scandinavian Wolves: Single Large or Several Small? *PLOS ONE*, 11 (12), e0168062. <https://doi.org/10.1371/journal.pone.0168062>
- Sand, H., Liberg, O., Wikenros, C., Åkesson, M., Zimmermann, B. & Wabakken, P. (2022). – effects of increased population size and culling.
- Sand, H., Wabakken, P., Zimmermann, B., Johansson, Ö., Pedersen, H.C. & Liberg, O. (2008). Summer kill rates and predation pattern in a wolf–moose system: can we rely on winter estimates? *Oecologia*, 156 (1), 53–64. <https://doi.org/10.1007/s00442-008-0969-2>
- Sand, H., Wikenros, C., Wabakken, P. & Liberg, O. (2006). Cross-continental differences in patterns of predation: will naive moose in Scandinavia ever learn? *Proceedings of the Royal Society B: Biological Sciences*, 273 (1592), 1421–1427. <https://doi.org/10.1098/rspb.2005.3447>
- Sand, H., Zimmermann, B., Wabakken, P., Andrèn, H. & Pedersen, H.C. (2005). Using GPS technology and GIS cluster analyses to estimate kill rates in wolf—ungulate ecosystems. *Wildlife Society Bulletin*, 33 (3), 914–925. [https://doi.org/10.2193/0091-7648\(2005\)33%5B914:UGTAGC%5D2.0.CO;2](https://doi.org/10.2193/0091-7648(2005)33%5B914:UGTAGC%5D2.0.CO;2)
- Sand, H., Zimmermann, B., Wabakken, P., Eriksen, A. & Wikenros, C. (2025). Quantifying large carnivore predation relative to human harvest on moose in an intensively managed boreal ecosystem. *Ecological Applications*, 35 (1), e70000. <https://doi.org/10.1002/eap.70000Digital>

- SFS 1987:259 Jaktlag
- Skogsstyrelsen. (2025). Viltskador på skog. <https://www.skogsstyrelsen.se/bruks-skog/skogsskador/viltskador/>. [31-05-2026]
- SLU Artdatabanken (2026a). Artfakta: älg (*Aces alces*). <https://artfakta.se/taxa/206046> [2026-05-12]
- SLU Artdatabanken (2026b). Artfakta: eurasiatisk skogsvarg (*Canis lupus lupus*). <https://artfakta.se/taxa/100024> [2026-04-30]
- Söderberg, A., Ågren, E. & Hård af Segerstad, C. (2010). Slutrapport från SVA:s undersökningar av de 28 vargar som fälldes under licensjakten 2010. Sveriges veterinärmedicinska Anstalt, SVA
- Söderberg, A., Åsbrink, J., Hård af Segerstad, C. & Ågren, E. (2011). SVA:s undersökningar av vargar fällda under licensjakten 2011. (18). Sveriges veterinärmedicinska Anstalt, SVA
- Solberg, E.J., Loison, A., Sæther, B. & Strand, O. (2000). Age-specific harvest mortality in a Norwegian moose *Alces alces* population. *Wildlife Biology*, 6 (1), 41–52. <https://doi.org/10.2981/wlb.2000.036>
- Statistiskmyndigheten SCB. (n.d). Statistikdatabasen. <https://www.statistikdatabasen.scb.se/pxweb/sv/ssd/> [07-05-2026]
- Storch, I., Tallian, A., Boitani, L., Di Bernardi, C., Kusak, J., Şekercioğlu, Ç., Smith, D., Vucetich, J. & Zimmermann, B. (2024). Wolves across borders. *Wildlife Biology*, 2024 (6). [https://doi.org/10.1002/wlb3.01417open\\_in\\_new](https://doi.org/10.1002/wlb3.01417open_in_new)
- SVA rapport (2018). *Licensjakt på varg 2018*. (SVA:s rapportserie, 47/2018). Statens veterinärmedicinska anstalt, SVA.
- SVA rapport (2021). *Licensjakt på varg 2021*. (65). Statens veterinärmedicinska anstalt.
- Svenska Jägareförbundet (2025). Den goda jaktetiken. <https://jagareforbundet.se/jakt/etik/den-goda-jaktetiken/> [10-06-2026]
- Svensson, L., Wabakken, P., Maartmann, E., Åkesson, M. & Flagstad, Ø. (2015). Inventering av varg vintern 2014-2015. Inventeringsresultat för stora rovdjur i Skandinavien. (1–2015)
- Svensson, L., Wabakken, P., Maartmann, E., Åkesson, M. & Flagstad, Ø. (2017). Inventering av varg vintern 2016-2017. Bestandsövervakning av ulv vintern 2016-2017. Bestandsstatus for store rovdyr i Skandinavia. Bestandsstatus för stora rovdjur i Skandinavien. (1–2017). Viltskadecenter, Institutionen för ekologi, Sveriges Lantbruksuniversitet.
- Svensson, L., Wabakken, P., Maartmann, E., Åkesson, M., Flagstad, Ø. & Hedmark, E. (2019). Inventering av varg vintern 2018-2019. Bestandsövervakning av ulv vintern 2018-2019. Bestandsstatus for store rovdyr i Skandinavia. Bestandsstatus för stora rovdjur i Skandinavien. (1–2019)

- Svensson, L., Wabakken, P., Maartmann, E., Cardoso Palacios, C., Flagstad, Ø. & Åkesson, M. (2021). Inventering av varg vintern 2020-2021. Bestandsovervakning av ulv vintern 2020-2021. Bestandsstatus for store rovdyr i Skandinavia. Bestandsstatus for stora rovdjur i Skandinavien. (1–2021)
- Svensson, L., Wabakken, P., Maartmann, E., Nordli, K., Flagstad, Ø., Danielsson, A., Hensel, H., Pöchhacker, K. & Åkesson, M. (2023). Inventering av varg vintern 2022-2023. Bestandsovervakning av ulv vintern 2022-2023. Bestandsstatus for store rovdyr i Skandinavia. Bestandsstatus for stora rovdjur i Skandinavien. (1–2023)
- Svensson, L., Wabakken, P., Maartmann, E., Nordli, K., Jensen, M. Ø., Milleret, C., Dupont, P., Bischof, R., Åkesson, M. & Flagstad, Ø. (2025). Bestandsovervakning av ulv vintern 2024 - 2025. Inventering av varg vintern 2024 – 2025. Bestandsstatus for store rovdyr i Skandinavia. Bestandsstatus for stora rovdjur i Skandinavien. (1–2025).
- Swedish Environmental Protection Agency - Naturvårdsverket (2016). Nationell förvaltningsplan for varg: förvaltningsperioden 2014-2019 (2016). Justerad version januari 2016. Naturvårdsverket.
- Swedish Environmental Protection Agency - Naturvårdsverket. (2018). Uppföljning av mål inom älgförvaltningen – Redovisning av regeringsuppdrag.
- Swedish Environmental Protection Agency - Naturvårdsverket (2010). Beslutet om licensjakt på varg 2010: en processutvärdering med fokus på beredningen av beslutet. (6361). Naturvårdsverket.
- Swedish Environmental Protection Agency - Naturvårdsverket (2022). Strategi for svensk viltförvaltning 2022-2029. Publikation, 2022–2029, 28
- Swedish Environmental Protection Agency - Naturvårdsverket. (2025a). Fastställande av miniminivåer for varg gällande rovdjursförvaltningsområden.  
<https://www.naturvardsverket.se/49cc14/contentassets/2589d7e5ee29443fa81039880e10868a/faststallande-av-miniminivaer-for-varg-2024-2026.pdf>
- Swedish Environmental Protection Agency – Naturvårdsverket. (2026). Jakt på varg.  
<https://www.naturvardsverket.se/amnesomraden/jakt-och-vilt/jakt-pa-rovdjur/jakt-pa-varg/> [2026-04-20]
- Swedish Environmental Protection Agency - Naturvårdsverket. (2025b). *Nya miniminivåer for varg*. (NV-25-011918). Naturvårdsverket.
- Uhlhorn, H., Åsbrink, J. & Söderberg, A. (2013). SVA:s undersökningar av vargar fällda under selektiv, riktad jakt 2013. (27)
- Wabakken, P., Sand, H., Liberg, O., Bjärvall, A. (2001). The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. *Canadian Journal of Zoology*. 79(4). 710-725.
- Wabakken, P., Svensson, L., Kojola, I., Maartmann, E., Strømseth, T.H., Flagstad, Ø. & Åkesson, M. (2014). Ulv i Skandinavia og Finland: Slutrapport for bestansavervakning av ulv vintern 2013-2014. (11–2014)

- Wabakken, P., Svensson, L., Kojola, I., Maartmann, E., Strømseth, T.H., Flagstad, Ø., Åkesson, M. & Zetterberg, A. (2013). Ulv i Skandinavia og Finland: Slutrapport for bestandsovervåkning av ulv vinteren 2012-2013. (5–2013)
- Wabakken, P., Svensson, L., Maartmann, E., Åkesson, M. & Flagstad, Ø. (2016). Bestandsovervåking av ulv vinteren 2015-2016. Bestandsstatus for store rovdyr i Skandinavia. (1–2016)
- Wabakken, P., Svensson, L., Maartmann, E., Åkesson, M. & Flagstad, Ø. (2018). Bestandsovervåking av ulv vinteren 2017-2018. Bestandsstatus for store rovdyr i Skandinavia. (1–2018)
- Wabakken, P., Svensson, L., Maartmann, E., Nordli, K., Flagstad, Ø., Danielsson, A., Cardoso Palacios, C. & Åkesson, M. (2024). Bestandsovervåking av ulv vinteren 2023-2024. Inventering av varg vintern 2023-2024. Bestandsstatus for store rovdyr i Skandinavia. Beståndstatus för stora rovdjur i Skandinavien. (1–2024)
- Wabakken, P., Svensson, L., Maartmann, E., Nordli, K., Flagstad, Ø. & Åkesson, M. (2020). Bestandsovervåking av ulv vinteren 2019-2020. Inventering av varg vintern 2019-2020. Bestandsstatus for store rovdyr i Skandinavia. Beståndstatus för stora rovdjur i Skandinavien. (1-2020.)
- Wabakken, P., Svensson, L., Maartmann, E., Nordli, K., Flagstad, Ø. & Åkesson, M. (2022). Bestandsovervåking av ulv vinteren 2021-2022. Inventering av varg vintern 2021-2022. Bestandsstatus for store rovdyr i Skandinavia. Beståndstatus för stora rovdjur i Skandinavien. (1–2022)
- Widemo, F. & Leonardsson, K. (2025). Älgstammens utveckling: älgförvaltningen i siffror jaktåret 2024/25. Institutionen för vilt, fisk och miljö, Sveriges lantbruksuniversitet. <https://doi.org/10.54612/a.4oh666kc2e>
- Widemo, F., Elmhagen, B. & Liljebäck, N. (2019). Viltets ekosystemtjänster: en kunskapsmanställning till stöd för värdering och förvaltning. (6889). Naturvårdsverket.
- Widemo, F., Leonardsson, K., Ó Cuív, C., Anderson, J. & Berndt, C. (2025). Utvärdering av de kvantitativa målen inom den svenska älgförvaltningen. (Rapport Skog). Fakulteten för skogsvetenskap, Sveriges lantbruksuniversitet. <https://doi.org/10.54612/a.4co3ohmkvd>
- Wikenros, C., Sand, H., Bergström, R., Liberg, O. & Chapron, G. (2015). Response of Moose Hunters to Predation following Wolf Return in Sweden. PLOS ONE, 10 (4), e0119957. <https://doi.org/10.1371/journal.pone.0119957>
- Wikenros, C., Sand, H., Di Bernardi, C. & Zimmermann, B. (2024). The role of predation, forestry and productivity in moose harvest at different spatial levels of management units. Wildlife Biology, 2024 (6), e01248. <https://doi.org/10.1002/wlb3.01248>
- Wikenros, C., Sand, H., Månsson, J., Maartmann, E., Eriksen, A., Wabakken, P. & Zimmermann, B. (2020). Impact of a recolonizing, cross-border carnivore population on ungulate harvest in Scandinavia. Scientific Reports, 10 (1), 21670. <https://doi.org/10.1038/s41598-020-78585-8>

- Wikenros, C., Zimmermann, B., Månsson, J., Eriksen, A., Wabakken, P. & Sand, H. (2025). Retrospective analyses to understand how wolf territory density impacts moose quotas, harvest and observation rate. *European Journal of Wildlife Research*, 71 (3), 42. <https://doi.org/10.1007/s10344-025-01920-9>
- Zimmermann, B., Sand, H., Wabakken, P., Liberg, O. & Andreassen, H.P. (2015). Predator-dependent functional response in wolves: from food limitation to surplus killing. Coulson, T. (red.) (Coulson, T., red.) *Journal of Animal Ecology*, 84 (1), 102–112. <https://doi.org/10.1111/1365-2656.12280>

# Popular science summary

When managing wildlife (animals living in the wild) in a human dominated landscape, conflicts between different interest groups could easily arise. If the wildlife populations get too dense, they can cause damage to human activities such as agriculture, forestry, domestic animal husbandry, reindeer husbandry and traffic safety. To minimise the populations of wildlife, hunting is commonly used, and it has a large recreational value and also provides high quality meat. Among the species that are legally allowed to be hunted in Sweden (game species), the moose is the most important one. Since 2012, the species is managed in smaller populations within so called moose management areas (MMA), where the MMAs can cross county borders if necessary. Wolves are managed via proactive- and protective hunting (hereafter culling), to minimise their population size and to protect for example livestock from depredation. Since 2015, the proactive culling has had the aim to kill all individuals within a wolf territory.

This study investigates if proactive culling of wolves would have an impact on the hunt (hereafter harvest) of moose. This by answering the two questions, does proactive culling of wolves result in a decrease in the density of wolves, and is there an increase in the harvest and density of moose, in a regional scale in south-central Sweden?

Harvest data of moose between the hunting years 2012/2013 – 2023/2024 from the counties Värmland, Örebro and Västmanland were used. The total harvest per MMA (per km<sup>2</sup>), the proportion of females out of adult harvest, and the proportion of calves out of the total harvest was analysed. A calculated index of the wolf territory density (a proxy for how high the density of wolves are within an area), the management goal of the moose population (if the management wanted their population to decrease, be unchanged or increase), and the moose density prior to the harvest (per km<sup>2</sup>) was compiled for all the MMAs. The MMAs was also sorted into if they have had culling of wolves or not (used as a control) within the study period. The analysis was done for two different time spans, a short (before and after culling) and a longer (three years before and three years after culling).

The main findings indicated that there was a direct impact on the density of wolves after culling was conducted, but it was weak. There was also a large difference in the wolf territory density depending on if the area had culling or was used as a control, with a higher territory density of wolves where culling is conducted. For the total harvest, the short time span resulted in no change, but in the longer time span there was a time-lagged response in increased moose harvest after culling of wolves, but it was weak. The proportion of females was not impacted by any of the variables included in the study. The proportion of harvested calves was higher in the control areas compared to the areas with culling, and the harvest did not have a drastic change with an increase in wolf territory density.

How large carnivores can co-exist with humans in the human dominated landscape will most likely always be questioned. The same with how the carnivores are managed. Depending on the public's view on the matter (here, carnivore existence), people in the society will always have different opinions and attitudes regarding the topic. With an increased knowledge, the conflicts might minimise, and the goal should be to make the management of carnivores and ungulates more convenient. The results from this study are useful for the continuous adaptive management of ungulates and carnivores in Sweden and likely also in other countries where wolves currently re-establish.

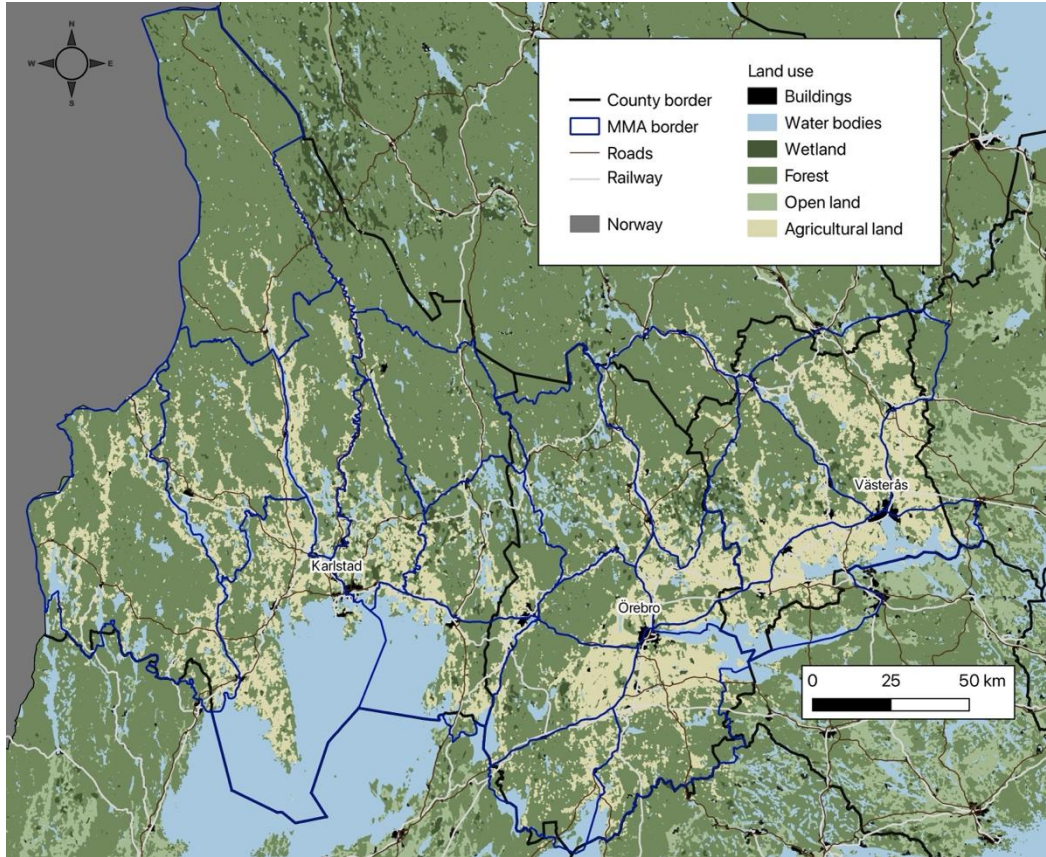
# Acknowledgements

First of all, I would like to thank my supervisor Camilla Wikenros for the opportunity to write my master's thesis with you at Grimsö Wildlife Research Station. It has been a great experience, and I have learnt a lot! I would like to thank my assistant supervisors; Håkan Sand, thank you for your support and feedback regarding the analysis and my writing, Fredrik Widemo, thank you for your help with getting in contact with the County Administrative Boards and helping me collect the correct data regarding the moose harvest. Thanks also to the County Administrative Boards in Värmland, Örebro and Västmanland who sent me all their management plans. I am also thankful for the Grimsö staff that gave me the opportunity to take part in some fieldwork outside of my thesis work.

I would also like to thank my bunker buddies and friends, especially Julia who has since day one been by my side through every high and low of this project. Lastly, thank you my dear family for always believing in me and for being my greatest supporters.

# Appendix A

Habitat map of Värmland, Örebro and Västmanland county.



## Appendix B

Table B1. A compilation of wolves killed in relation to licensed wolf hunt for period 2010-2014. Year, total number of killed individuals, age, sex and number killed within which County as well as if the hunt occurred or not is mentioned. The information is based on reports by SVA between 2010-2014.

Year	Tot.	County					Age		Sex	
		W	X	S	O	T	Adult	Yearling*	F	M
2010	28	10	3	9	3	3	18 + 1'	9	15	13
2011	19	6	3	6	2	2	15	4	8	11
2012	No wolf culling this year									
2013**	3	2				1		3	1	2
2014	No wolf culling this year									

\*Born previous year (<1 year old)

'Uncertain about age

\*\* Licensed wolf hunt stopped after a few individuals were shot

County letters: W = Dalarna County, X = Gävleborg County, S = Värmland County, O = Västra Götaland County and T = Örebro County

Table B2. A compilation of wolves killed in relation to licensed wolf hunt for period 2015-2025. Year, age, sex, total number of killed individuals and information about which County, territory and how many were killed is mentioned. The information is based on reports by SVA between 2015-2025.

Year	Tot.	Licenced hunting				Age		Sex	
		County	Territory name	Approved to hunt	No. killed	Adult	Yearling*	F	M
2015	44	S – H1	Medskogen/Kläggen	H1+H2 = 24	24	7	17	11	13
		S – H2	Gårdsjö/Forshaga						
		T		-	12	6	6	6	6
		U		-	8	5	3	5	3
2016	14	W	Lövsjö	8	7	3	4	1	6
		X	Åmot/Ockelbo	8	7	3	4	3	4
		U	Färna	6	-	-	-	-	-
		S/T	Loka	6	-	-	-	-	-
		S	Vimyren, Brattfors/Sandasjön	20	-	-	-	-	-
2017	25	W	Orsen	6	6			3	3
		X	Blyberg	6	6			3	3
		S/T	Loka	7	7			3	4
		S	Brattfors	6	6			2	4
2018	15	W	Flaten	6	5	4	1	2	3
		X	Nyskogen	2	2	2	-	1	1
		S	Vimyren	6	2	2	-	1	1
		U	Kölsta	6	6	3	3	2	4
		T	Kindla	2	-	-	-	-	-

2019		Hunt stopped due to small population							
2020		Hunt stopped due to small population							
2021	27	X	Andån	6+4	10	4	6	4	6
		X	Ryssjön	6	6	3	3	3	3
		S	Stora Bör	6	6	1	5	2	4
		U/T	Vidaln	6	5	4	1	1	4
2022	28	X/W	Gullsjön	6	3	2	1	3	-
		X	Skottmyren	6	5	2	3	2	3
		W/U/T	Snösjön/Haraldsjön	14	12	8	4	5	7
		S/T	Immen	6	6	3	3	4	2
		S	Römskog	3	2	1	1	2	-
2023	57	X	Ödmården/Mörtsjön	10	3	2	1	1	2
		X/W	Tinäset	8	2	2	-	1	1
		S	Juvberget/Ulvåa	12	7	2	5	4	3
		S	Kockohonka	6	6	3	3	3	3
		S	Skacksjö	6	6	1	5	3	3
		S	Flatmossen	6	2	2	-	1	1
		S	Forshaga	6	6	5	1	5	1
		S/T	Vismen	6	6	4	2	3	3
		T	Ölen	6	3	3	-	2	1
		T	Grecken	6	6	2	4	2	4
		U	Venabäcken	6	6	2 + 1'	3	2	4
		U/T/W	Almhöjden	6	4	2 + 1'	1	2	2
2024	35	D	Gryten	6	5	5	-	2	3

		S	Tjunken	6	5	2	3	2	3
		U	Venabäcken	6	6	1	5	3	3
		O	Ripelången	6	6	3	3	3	3
		T	Tingeråsa	6	6	3	3	2	4
		T	Villingsberg	6	7	4	3	4	3
2025	25	S	Salungen	6	1	1	-	1	-
		U	Kesberget	6	6	3	3	3	3
		O	Klyftamon	6	6	3	3	4	2
		T	Mjuggsjön	6	6	4	2	2	4
		T	Tiveden	6	6	4	2	3	3

\*Born previous year (<1 year old)

'Uncertain about age

**Red text** = Decision overturned by the court of administrative law in Uppsala and Karlstad.

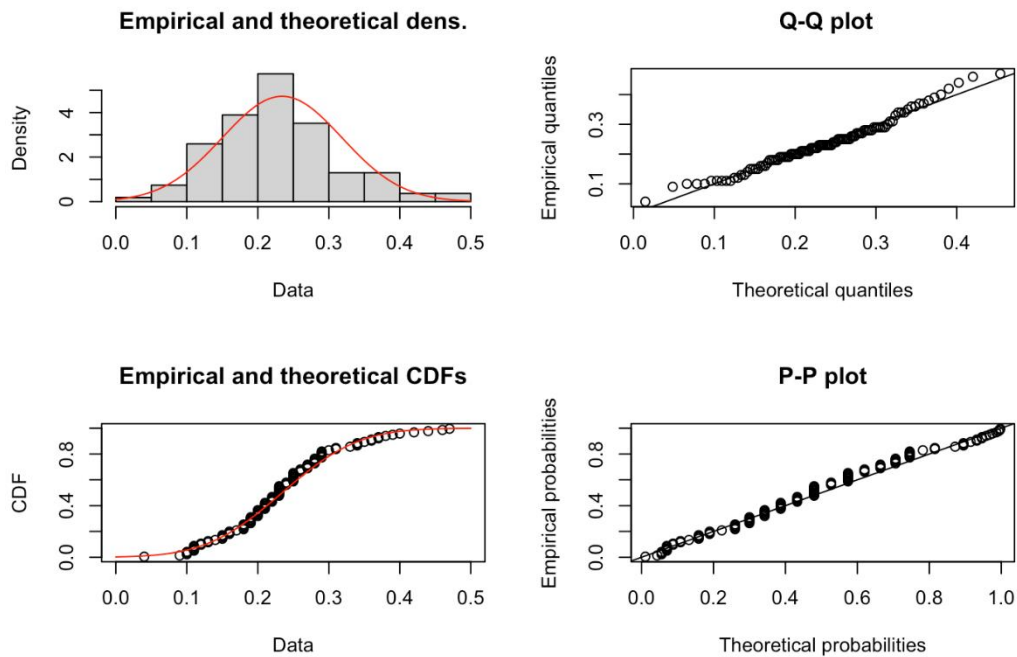
**Blue text** = Territory shared with Norway, total allocation of 18 wolves for both counties.

H1 + H2 = Hunting area 1 and 2

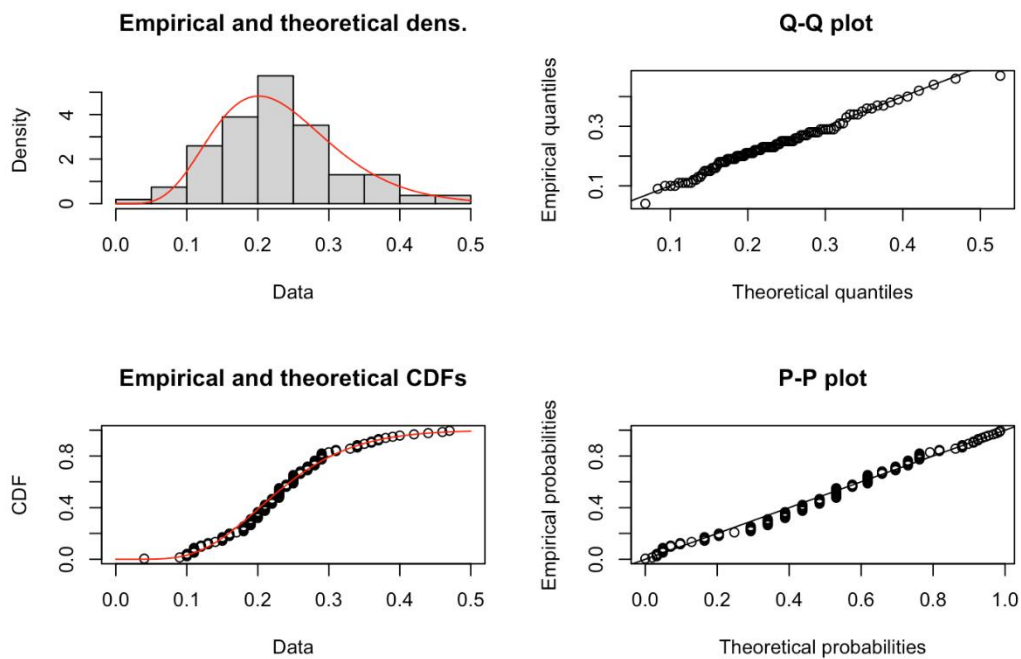
County letters: X = Gävleborg County, W = Dalarna County, S = Värmland County, O = Västra Götaland County, T = Örebro County, U = Västmanland County, D = Södermanland County

# Appendix C

A normally distribution test for the moose harvest values. Shapiro-Wilks test,  $p = 0.0635$ . Data not well fitted as normally distributed.

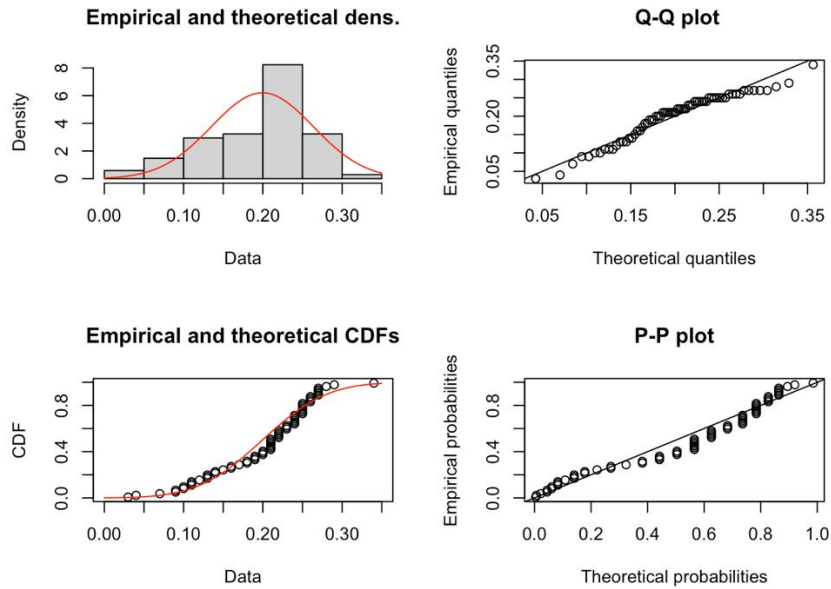


A gamma distribution test for the moose harvest values. Better fit compared to the normally distribution. The empirical and theoretical density of the data follows the right skewed data.

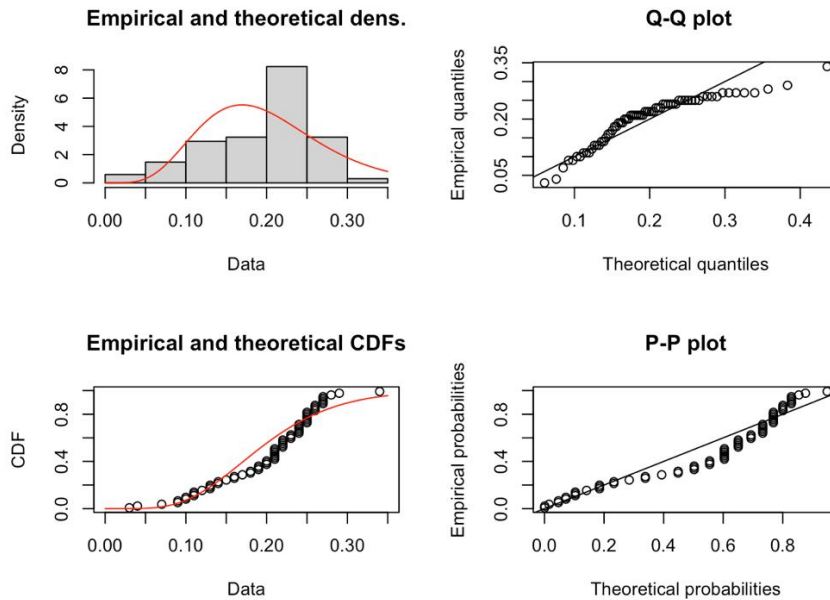


# Appendix D

A normally distribution test for the moose harvest values, for dataset one year before and one year after the harvest. Shapiro-Wilks test,  $p = 0.0041$ . Data not well fitted as normally distributed.



A beta distribution test for the moose harvest values, for dataset one year before and one year after the harvest. Better fit compared to the normally distribution.



## Appendix E

Table E1. Mean total harvest of moose per km<sup>2</sup> between the start of study 2012/2013 and end of study 2023/2024 within study area, Värmland, Örebro and Västmanland.

<b>County</b>	<b>Treatment</b>	<b>2012/2013</b>	<b>2023/2024</b>	<b>% change</b>
Värmland	Control	0.465	0.18	(-) 61.3
	Culling	0.373	0.2	(-) 26.4
Örebro	Control	0.36	0.0933	(-) 74.1
	Culling	0.31	0.108	(-) 65.3
Västmanland	Control	0.275	0.095	(-) 65.5
	Culling	0.28	0.14	(-) 50.0

## 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/sv/faq/228316>

YES, I, Ida Hopia Ivarsson, have read and agree to the agreement for publication and the personal data processing that takes place in connection with this.

NO, I/we do not give my/our permission to publish the full text of this work. However, the work will be uploaded for archiving and the metadata and summary will be visible and searchable.