

# Population and management models for the Swedish wild boar (*Sus scrofa*)

*Madeleine Magnusson*



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Populations- och förvaltningsmodeller för Sveriges vildsvin (*Sus scrofa*)

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**Credits:** 30 ECTS (hp)

**Level:** Advanced D

**Course title:** Independent project/ Degree project in Biology D

**Course code:** EX0564

**Programme:** Natural Resources Programme - Biology and Soil Science  
(Naturresursprogrammet – biologi och mark)

**Place of publication:** Uppsala/Grimsö

**Year of publication:** 2010

**Title of series:** Master's thesis, Department of Ecology

**Serial no:** 2010:18

**Cover:** Markus Schroeder

**Online publication:** <http://stud.epsilon.slu.se>

**Key Words:** wild boar, *Sus scrofa*, population models, growth rate, harvest strategies,  
management

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## Abstract

The wild boar *Sus scrofa* population in Sweden has increased rapidly in the last decades which has led to conflicts among stakeholders, for example due to crop damages in agriculture. Thus, there is an urgent need of quantified goals and effective strategies for wild boar management. To develop such strategies, knowledge on population dynamics is fundamental. In this study a deterministic matrix model was used to estimate population growth, based on previously published data. The exponential growth rate for a wild boar population was calculated to 1.48. Elasticity analysis indicated that a change in juvenile survival has the strongest potential impact on population growth. With the present Swedish population estimated to at least 150 000 wild boar and the growth rate 1.48, a net increase of 72 000 boar has to be shot annually to keep the population at equilibrium. Further, harvest simulations were made to investigate the effects of varied cull among animal categories on growth rate and total harvest levels. In a model where proportional harvest of adult females was increased from 0.0 to 0.4 (combined with harvest of juveniles), the total harvest needed for a stable population decreased with 45 %. The corresponding model using adult males resulted in higher harvest levels. The effect on growth rate from varying combinations of proportional harvest of juveniles and of adult females was also illustrated by contour curves for  $\lambda$  at different levels (increase-stable-decrease population). However, implementation of theoretically developed strategies meets various obstacles, when e.g. ethics and practical issues are considered, and such applied aspects were discussed.

*Key words: wild boar, Sus scrofa, population models, growth rate, harvest strategies, management*

## Sammanfattning

Vildsvinet har tidigare varit utrotat i Sverige, men återintroducerades under 1980-talet. Idag finns stadiga och växande vildsvinstammar i södra delen av landet, och populationen uppskattas bestå av totalt minst 150 000 djur. Den kraftiga ökningen speglas i avskjutningen, som ökat från ca 500 djur under 1990 till närmare 50 000 under 2009, liksom trafikolyckorna med vildsvin som under 2009 uppgick till 3000 rapporterade olyckor. I områden med täta populationer av vildsvin uppstår ofta problem och konflikter, då arten å ena sidan är ett populärt jaktvilt men som förorsakar skador och kostnader inom exempelvis jordbruket. Vildsvinen har kapacitet att föröka sig mycket snabbt vid fördelaktiga förhållanden, och jakttrycket har hittills inte motsvarat denna förökningstakt. Olika samhällsaktörer framställer idag påtryckningar om en intensifierad jakt på vildsvin för att minska antalet djur och därmed skadorna. För att kunna balansera stammarna till lokalt lämpliga nivåer på ett effektivt sätt behövs kunskaper om artens ekologi och hur de påverkas av olika förvaltningsinsatser. Syftet med denna studie var därför att göra uppskattningar av den svenska vildsvinsstammens tillväxttakt samt prognoser för dess utveckling utifrån olika förvaltningsscenarioer. Detta har gjorts med hjälp av matematiska modeller baserade på uppgifter om överlevnad och reproduktionsförmåga samt köns- och ålderssammansättningen i populationen.

Tillväxttakten för vildsvinspopulationen uppskattades till 48 % per år om man bortser från dödligheten av jakt. Baserat på denna ökningstakt beräknades att 72 000 djur skulle behöva skjutas årligen för att hålla populationen på dagens nivå (150 000), om man antar att urvalet (av kategorier djur) i jakten sker slumpmässigt. Med en fortsatt avskjutningsnivå på omkring 50 000 djur årligen, skulle populationen enligt dessa skattningar fördubblas på mindre än fyra år. Om däremot köns- och ålderssammansättningen i populationen förändras, till exempel på grund av jaktstrategin, så förändras även ökningstakten. För att undersöka utfallet av olika strategier gjordes modeller där jakttrycket på olika djurkategorier varierades, men med målet att hålla populationen stabil vid olika storlekar. Utfallet från sådana strukturerade modeller, som skiljer sig från den enkla varianten ovan, visar exempelvis att ett ökat jakttryck på vuxna hondjur leder till en betydande minskning av tillväxttakten och därmed sänkt total avskjutning. En jakt som i motsvarande grad inriktar sig på att skjuta vuxna handjur skulle leda till att den totala avskjutningen ökar, eftersom en hög andel av årsreproduktionen också måste skjutas om populationen ska hållas konstant. Om jakten endast inriktades på hondjur äldre än ett år blev den totala avskjutningen 14 500, medan nivån hamnade på 59 000 djur om enbart 0-1 åringar sköts. En slutsats av min studie är att valet av förvaltningsstrategi har en avgörande betydelse för den totala avskjutningsnivån då vildsvinsstammen är stor. Även om matematiska samband kan ge bra och begriplig information om hur en population påverkas av olika åtgärder, är sådana modeller inte alltid enkla att omsätta i praktiken. Det är till exempel svårt att göra säkra köns- och åldersbestämning av vildsvin, särskilt i snabba jaktsituationer eller vid dåligt ljus (vakjakt). Jakt inriktad mot hondjur är överlag problematisk, eftersom sugga med kulningar är fredade och ledarsuggor inte bör skjutas då det kan resultera i grupper som leds av oerfarna djur. Ett högt jakttryck på de unga djuren kan följaktligen vara mer lämpligt ur praktiska och etiska synvinklar, men det kräver å andra sidan en hög totalavskjutning för att hålla populationen stabil. Det finns många faktorer att beakta för att formulera lämpliga mål för förvaltningen och lämplig storlek för stammen. Förutom näringsmässiga aspekter på skadenivåer, är det ur praktiskt hänseende även högst relevant att ta hänsyn till vilka avskjutningsnivåer som jägare på frivillig basis kan upprätthålla.

*Nyckelord: vildsvin, Sus scrofa, populationsmodeller, populationstillväxt, beskattningsstrategier, förvaltning*

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## Introduction

A rapid increase of wild boar (*Sus scrofa*) population densities and distribution has been observed in Europe in recent decades (Sáez-Royuela & Tellería 1986, Geisser & Reyer 2005). Wild boar is now the most widespread and second most abundant ungulate in Europe (Herrero et al. 2008, Apollonio et al. 2010). In historical times, the native occurrence of wild boar in Norway and Sweden extended up to 60° N (Briedermann 1990). In Sweden, the species was hunted to extinction by the end of the 18<sup>th</sup> century due to its damage to agricultural land. After being reintroduced and extinct a few times, the present wild boar population in Sweden descends from animals escaped from enclosures in the 1970's and probably from illegal releases (Anon. 2010a, Jägareförbundet 2010a). In 1988, the Swedish parliament decided that the species should be considered as native and a Swedish population should thus be maintained (Anon. 2010a). Since then, the free-living population has increased rapidly in size and distribution. Today the wild boar is established in the southern part of Sweden (south of highway E18 and the river Dalälven), and is expected to expand further, at least within the present range in coming years (Anon. 2007).

Possible causes for the rapid increase are e.g. variations in type of dominant agricultural crops; climatic changes resulting in higher temperatures and less snow cover; increased frequency of mast seeding where oak and beech are abundant; reintroductions and rapid dispersal due to human activities; lack of predator species (wolf *Canis lupus*) in many areas; the fact that newly established, small populations may increase without negative effects of density dependence and finally, a low hunting pressure (Sáez-Royuela & Tellería 1986, Jedrzejewska et al. 1997, Leaper et al. 1999, Geisser & Reyer 2005). Moreover, there is a possibility that supplemental feeding has contributed to the observed increase in population densities (Bieber & Ruf 2005, Geisser & Reyer 2005). Food from feeding stations made up the majority of the stomach content in examined wild boar from a study in Sweden (Lemel 1999). However, the effects of feeding are unclear and not studied in order to evaluate its impact on population dynamics (Lemel 1999, Náhlik & Sándor 2003, Geisser & Reyer 2004, Geisser & Reyer 2005, Holmgren 2009). Furthermore, wild boar holds the highest potential reproductive rate among all ungulate species in relation to body-mass (Lemel 1999, Geisser & Reyer 2005). Mortality of wild boar in Sweden is predominantly attributed to hunting (Lemel 1999). Predators have most impact on mortality of piglets and yearlings and wolf is an important predator when the distributions overlap (Baskin & Danell 2003). However, present ranges of wild boar and wolf in Sweden are barely overlapping (Anon. 2009, Anon. 2010b).

Wild boar is a species which in many parts of the world is considered problematic, because of its negative consequences for agriculture (Sáez-Royuela & Tellería 1986, Neet 1995, Leaper et al. 1999, Bieber & Ruf 2005), which is the case also in Sweden (Anon. 2010a). Vehicle collision with wild boar is another growing problem, with more than 3000 accidents reported in Sweden year 2009, and a mean annual increase of 29 % from 2003 to 2009 (Nationella viltolycksrådet 2010).

To decrease the population growth and prevent crop damage, management of wild boars has in recent years focused on facilitating high hunting pressure. Feeding is widely used in the entire distribution range for three purposes: to increase growth rate and density, as bait for an effective hunting, and to distract animals from agriculture fields (Lemel 1999). The length of the hunting season for wild boar is generous and cannot be further extended, due to the risk of shooting adult females from their young. Since 2009, fixed light at the bait is allowed, and special permissions for using night vision sensor can also be obtained from County boards to

make the hunt safer and easier (Naturvårdsverket 2009a). In 2010 the Swedish Environmental Protection Agency (EPA) presented a management plan for wild boar, with focus on reducing damage by decreasing the population (Anon. 2010a). Although various measures have been taken (above), the problems experienced by e.g. farmers are far from solved in many regions. The present situation in Sweden, as well as in other countries, has accentuated the need for effective management strategies for the species.

When deciding for a strategy to manage the size of a wildlife population, knowledge about population dynamics of the species is essential. Mathematical models can be used as a tool to predict future population size and the outcome of varying management strategies. Population modeling of mammal populations has mainly been practiced for threatened or rare species, e.g. large carnivores, and for game species with economic importance like deer, for example to estimate maximum sustainable yields (Brooks & Lebreton 2001, Hauser et al. 2006). Population models can also be used to optimize harvest with the purpose of controlling the expansion or lower population size of a species.

One frequently used technique for modeling population dynamics is the use of matrix models. The rate of change in population size is determined by rates of birth/death and immigration/emigration. The rates of birth and death (vital rates) usually vary with age and sex. As a consequence, to predict the annual change in population size not only an estimate of the current population size is needed but also the age and sex distribution. Regulation of a population can be accomplished by a random, fixed or proportional harvest of the population. An alternative approach is to deliberately change population composition and consequently the rate of increase. Sensitivity and elasticity analysis, which estimates the effect of changes in vital rates on population growth rate, can be used to point out the vital rate(s) that are most effective to focus on in order to change the population as desired (Benton & Grant 1999).

In studies of wild boar population dynamics and growth rates, implications for management is a frequently discussed issue (Neet 1995, Goulding et al. 2003, Bieber & Ruf 2005, Toïgo et al. 2008). However, to my knowledge only one attempt, by Bieber & Ruf (2005), has been made to model population pest-control measures for areas with rapidly expanding wild boar populations. Bieber & Ruf (2005) focused on growth rate sensitivity to vital rate parameters that vary with environmental conditions, in order to develop management strategies for pulsed resource consumers. Several attempts to estimate population size, growth rate and required harvest levels for wild boar in Sweden have been made (Lemel 1999, Lemel & Truvé 2008, Jägareförbundet 2010a), but no population modeling or simulations including different harvest strategies.

In this study, I constructed deterministic matrix population models, based on previously published data on vital rates for wild boars. The aim was to predict the development of the wild boar population in Sweden under varying harvest scenarios. I made simulations to investigate to which extent varying harvest strategies affect the population growth, and the harvest level necessary to reach given management goals for the population. Finally, I discuss the possible implications for the management of wild boar in Sweden.

## Methods

### Estimation of population size

According to a recent study the present Swedish population probably encompass at least 150 000 wild boar in 2009/10 (Jansson et al. 2010). From that, I chose three levels of initial and post-harvest population sizes, namely: 150 000, 250 000 and 350 000. The mean value of the annual increase after harvest for the years 2000-2009, estimated from hunting statistics, was 31 % (assuming fixed harvest strategy and sex and age composition; Jansson et al. 2010).

### Estimation of vital rates

I reviewed literature for data on fecundity and survival of wild boar to use in the models (Table 1). I used data on number of fetuses and proportion of reproducing females from the Swedish study by Lemel (1999), and assumed that the mean number of fetuses represent mean litter size. No significant difference was found between mean number of fetuses of yearlings and adult females (Lemel 1999, and see Table 1). Wild boar under good food supply is capable of reproducing even during the first year (Ahmad et al. 1995, Lemel 1999, Bieber & Ruf 2005, Herrero et al. 2008). I assumed each female mate only once a year. Fecundity represents the stage-specific reproductive contribution, weighted by survival probability of breeders.

Table 1. Summary of vital rates and age composition in wild boar populations used in the models.

|          | Mean number of fetuses <sup>(1)</sup> | Proportion reproducing <sup>(1)</sup> | Survival rate female ( $P_f$ ) <sup>(2)</sup> | Survival rate male ( $P_m$ ) <sup>(2)</sup> | Fecundity ( $F$ ) | Age composition % <sup>(3)</sup> |
|----------|---------------------------------------|---------------------------------------|---|---|-------------------|----------------------------------|
| Juvenile | 2.50                                  | 0.25                                  | 0.78  | 0.73  | 0.24              | 46                               |
| Yearling | 4.35                                  | 0.60                                  | 0.82  | 0.68  | 1.07              | 24                               |
| Adult    | 4.35                                  | 0.60                                  | 0.81  | 0.77  | 1.06              | 30                               |

(1) Lemel 1999

(2) Focardi et al. 2008, Toigo et al. 2008

(3) Appendix I

Sex ratio for all ages is on average 1:1 (Leaper et al. 1999, Bieber & Ruf 2005), which was assumed in my models as well. The age composition I used as input for the models was compiled by calculating the mean values from 11 studies in 11 countries in Europe and North/Central Asia (Appendix I). Data on survival rates excluding hunting mortality for the Swedish wild boars was not available. The annual survival rates used in my models was instead obtained by calculating the mean values for the natural mortality in harvested wild boar populations, presented by Focardi et al. (2008) and by Toigo et al. (2008). The age specific survival from these studies and tree others are shown in Figure 1.

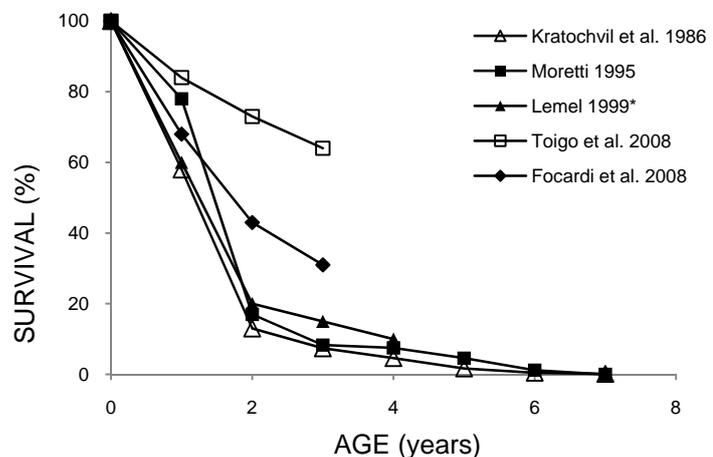


Figure 1. Age-specific survival of wild boar in harvested populations. Data from Toigo et al. (2008) and Focardi et al. (2008) consider only the natural mortality.

\*Estimate from summary and figure. Postnatal mortality is not included.

## Population growth rate

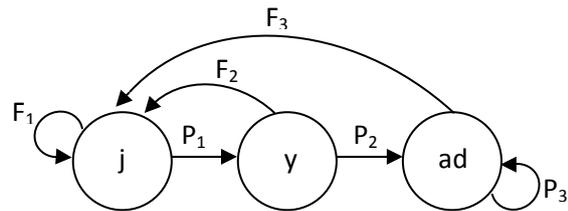
To compute the population growth rate ( $\lambda$ ) I used a deterministic matrix model. Here only the female population was modeled, assuming that males have no impact on growth rate and the sex-ratio is 1:1. Available data on vital rates for wild boar mainly differs between the age-classes 0-1, 1-2 and older than 2 years old (Lemel 1999, Focardi et al. 2008, Toïgo et al. 2008). Thus, I considered a stage-structured population with the three categories juvenile, yearling and adult, as illustrated in Figure 2. I assumed no migration at the national level and no effects of density dependence. The population size and stage structure at time  $t+1$  can be computed by multiplying a vector  $N$  describing the stage-specific population at time  $t$  by the projection matrix  $A$ :

$$N_{t+1} = AN_t \quad (1)$$

$$\text{where } A = \begin{bmatrix} F_1 & F_2 & F_3 \\ P_1 & 0 & 0 \\ 0 & P_2 & P_3 \end{bmatrix} \quad \text{and} \quad N = \begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}$$

and where, for stage  $i$ ,  $P_i$  = stage-specific survival in females,  $F_i$  = stage-specific fecundity and  $N$  = the population at post-breeding year  $t$ . Parameter values are listed in Table 1. The non-zero value at  $P_3$  represents the probability of surviving and remaining within the adult stage. The population growth rate was given by the largest eigenvalue ( $\lambda$ ) of the matrix. Sensitivity and elasticity of  $\lambda$  to the matrix elements was computed (De Kroon et al. 2000; Software R 2.10.1).

Figure 2. Life cycle graph for a wild boar population, representing the stages 1, juveniles (0-1 years); 2, yearlings (1-2 years); 3, adults (>2 years); (F), stage-specific fecundity; (P), stage-specific survival.



After a number of iterations the population reaches a stable stage-distribution  $\mathbf{w}$  (left eigenvector), and settles into exponential growth with the annual rate of increase,  $\lambda$ . When this state is reached, the matrix equation (1) corresponds to the equation:

$$N_{t+1} = N_t \cdot \lambda \quad (2)$$

which was used to project population size ( $N$ ) over time, compared with that for other growth rates (Figure 3).

## Harvest of the population

### Non-structured model with harvest

I computed the annual harvest ( $H_{eq}$ ) required to maintain an equilibrium population size ( $N_{eq}$ ) by:

$$H_{eq} = (\lambda - 1)N_{eq} \quad (3)$$

which assumes a stable stage-distribution ( $\mathbf{w}$ ) according to the deterministic matrix model above, and the sex-ratio 1:1. Further, the model implies a random harvest strategy, where categories of animals are harvested relative to their proportion in the population and that reproduction takes place before harvest. I also calculated the predicted population size in year

2015 and 2020 under varying harvest levels, according to this model. To show the range of possible harvest levels due to variable conditions, the net increase for growth rates in intermediate and good environmental conditions according to Bieber & Ruf (2005) was calculated.

### ***Population distribution, density and amount of hunters***

The present distribution area of wild boar was estimated as all counties with reports of wild boar harvested, together with the assumption that the distribution will be restricted to south of Limes Norrlandicus, due to unfavorable temperature and snow conditions for wild boar in the boreal zone (Fransson 1965, Baskin & Danell 2003, Anon. 2009). Therefore, areas north of Limes Norrlandicus where hunting was reported were not included here (Anon. 2009). The 15 counties included are listed in Appendix II. I estimated the amount of available wild boar habitat in the present geographical range to 114 779 km<sup>2</sup>, by summarizing the area of the following land use categories: agricultural land, forest land, and natural grasslands, heath land etc. (Anon. 2008). Amount of hunters in the same area was 188 581, defined as number of hunting permits in year 2005/06 (Mattsson et al. 2008). Given this distribution area for Swedish wild boars, I estimated population density for three levels of initial population size (150, 250 and 350 000), as well as the number of wild boar to shoot per hunter in order to maintain the population sizes, respectively, over time.

### ***Sex- and stage structured model with harvest***

To model different harvest strategies, I modified the above matrix model. The population was divided into juveniles, adult females and adult males (i.e. adult includes yearlings here). Survival of adults was calculated as the mean value of survival for yearlings and adults (see above). Survival probabilities for each sex- and age class ( $P_{ij}$ ) were multiplied by the proportion of respective category surviving after harvest ( $1 - h_{ij}$ ), where  $h$  is proportion harvested. Sex-ratio for harvested juveniles was assumed to be 1:1, i.e.  $h_{jf} = h_{jm}$ . In these harvest models the mortality is additive, as in the study by Toïgo et al. (2008).

The vector  $N$  was multiplied by a new matrix,

$$\mathbf{A} = \begin{bmatrix} F_j(1 - h_j) & F_{ad}(1 - h_f) & 0 & 0 \\ P_{jf}(1 - h_j) & P_{adf}(1 - h_f) & 0 & 0 \\ F_j(1 - h_j) & F_{ad}(1 - h_f) & 0 & 0 \\ 0 & 0 & P_{jm}(1 - h_j) & P_{adm}(1 - h_m) \end{bmatrix} \text{ where } \mathbf{N} = \begin{bmatrix} n_{jf} \\ n_{adf} \\ n_{jm} \\ n_{adm} \end{bmatrix}$$

for each time interval  $t$  to achieve equilibrium at given population sizes. Harvest of adult males was fixed at  $h_m = 0.3$ . Proportional harvest of adult females was fixed at  $h_f = 0.0, 0.1, 0.2, 0.3$  and  $0.4$  to simulate five different management scenarios. Harvest of juveniles was varied to reach an annual growth for the population close to  $\lambda = 1$ . Finally, I defined the harvest level of adult females required to maintain the population size if nothing but adult females was harvested. The same method was applied to a matrix where harvest of adult males was fixed at  $h_m = 0.0, 0.1, 0.2, 0.3$  and  $0.4$ . I used two approaches, with harvest of adult females fixed at  $h_f = 0.0$  and  $0.15$  respectively. Further, I used the above matrix to draw population growth rate contour curves as a function of proportional harvest of juveniles and adult females. Harvest of adult males was fixed again at  $0.3$ . For values of  $h_f$  and  $h_j$  ranging between 0 and 1, the dominant eigenvalue, here  $\lambda$ , of the matrix was computed (Software R 2.10.1).

If nothing else is specified, calculations were performed in Microsoft Excel 2007.

## Results

### Population growth rate

The growth rate of the wild boar population, estimated from the projection matrix  $A$  in equation 1 with vital rates according to Table 1, was  $\lambda = 1.48$ . This equals an average annual increase of 48 %. The population was more than doubled in numbers after two years with unlimited exponential growth. The projected population size in five years was one million and in ten years 7.5 millions, with an initial population of 150 000. The stable age distribution ( $w$ ) with 46 % juveniles, 24 % yearlings and 30 % adults, was reached in year three, assumed the initial age distribution used here (Table 1).

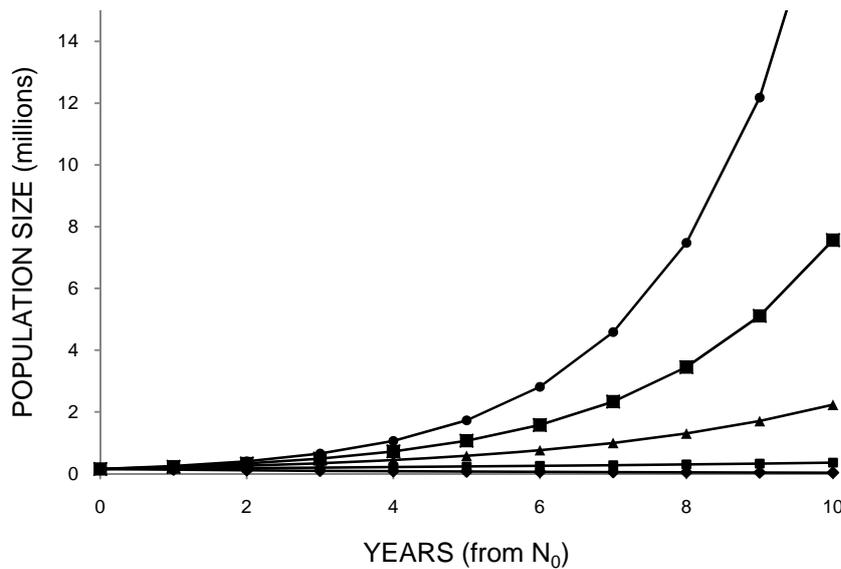


Figure 3. Projected population size over the following 10 years for a wild boar population, given a population size of 150 000 at year 0 with the annual increase  $\lambda = 1.48$  (■) or the annual increase  $\lambda = 1.31$  estimated from hunting statistics in Sweden (▲). Population growth for a wild boar population in poor, intermediate and good environmental conditions with  $\lambda = 0.85$  (◆),  $\lambda = 1.09$  (■) and  $\lambda = 1.63$  (●) respectively, calculated by Bieber & Ruf (2005).

Elasticity analysis showed that survival of juveniles,  $e(P_1)$  and adults,  $e(P_3)$  had the highest elasticity values and thus, if varied, the largest impact on population growth,  $\lambda$  (Table 2).

A 1 % decrease in juvenile survival will lower  $\lambda$  by 0.294 %, while a 1 % decrease in adult survival will lower  $\lambda$  by 0.193 %. Addition of  $e(P_2)$  and  $e(P_3)$  gives a total of 0.354, which means that a decrease in both yearling and adult survival by 1 % result in 0.354 % lowering of  $\lambda$ . Among reproduction parameters, adult fecundity,  $e(F_3)$  had the largest elasticity.

Table 2. Sensitivities ( $s$ ) and elasticities ( $e$ ) of  $\lambda$  to changes in vital rates in wild boar. For parameter values, see Table 1 and the corresponding matrix in equation 1.

| Elasticity |       | Sensitivity |       |
|------------|-------|-------------|-------|
| $e(P_1)$   | 0.294 | $s(P_1)$    | 0.559 |
| $e(P_2)$   | 0.161 | $s(P_2)$    | 0.291 |
| $e(P_3)$   | 0.193 | $s(P_3)$    | 0.354 |
| $e(F_1)$   | 0.058 | $s(F_1)$    | 0.352 |
| $e(F_2)$   | 0.134 | $s(F_2)$    | 0.185 |
| $e(F_3)$   | 0.161 | $s(F_3)$    | 0.225 |

## Harvest of the population

### *Non-structured model with harvest*

The annual net increase needs to be removed in order to stabilize the population at the same level as previous year. The net increase was 72 000, 120 000 and 168 000, respectively, for the three equilibrium population sizes (Table 3). Conversely, if a bag limit of 50 000 annually was set, the corresponding equilibrium population size ( $N_{eq}$ ) would be just about 105 000.

### *Population distribution, density and amount of hunters*

Bag per hunter at a harvest level of 72 000 wild boar was 0.38, which can be compared to 0.46 roe deer and 0.32 moose shot per hunter in the entire country in 2005/06 (Anon. 2006, Mattsson et al. 2008; Table 3). Population density varies between 13-30/1000 ha in the present distribution area, depending on desired equilibrium population size (Table 3).

Table 3. Harvest statistics required to maintain a wild boar population at equilibrium for different population sizes, given different rates of increase. Population density of wild boar within the present distribution area of 114 779 km<sup>2</sup> in Sweden and mean number of wild boar to shoot per hunter in the same area, with the net increase given  $\lambda = 1.48$ .

| N       | Harvest                     |                        |                           | Population density |
|---------|-----------------------------|------------------------|---------------------------|--------------------|
|         | $\lambda = 1.09-1.63^{(1)}$ | $\lambda = 1.48^{(2)}$ | bag/hunter <sup>(3)</sup> | /1000 ha           |
| 150 000 | 13 500 - 94 500             | 72 000                 | 0.38                      | 13                 |
| 250 000 | 22 500 - 157 500            | 120 000                | 0.64                      | 22                 |
| 350 000 | 31 500 - 220 500            | 168 000                | 0.89                      | 30                 |

<sup>(1)</sup> Rates of increase in intermediate and good environmental conditions, according to Bieber & Ruf (2005).

<sup>(2)</sup> Rate of increase according to the results in this study.

<sup>(3)</sup> Harvest specified for  $\lambda = 1.48$

Table 4. Projected population size in five and ten years given an initial population size of 150 000 in 2010 and a mean population growth of 1.48, for varying harvest levels.

| Year | Annual harvest |           |         |
|------|----------------|-----------|---------|
|      | 50 000         | 60 000    | 70 000  |
| 2015 | 429 621        | 302 521   | 175 420 |
| 2020 | 2 415 159      | 1 385 542 | 355 924 |

### *Sex- and stage structured model with harvest*

For the five management strategies modeled and an initial population size of 150 000, the harvest ranged between 14 500 with only adult females harvested, to just about 59 000 with no adult females harvested (Figure 4 A). Thus a higher proportional harvest of adult females resulted in a substantial reduction in total harvest required, according to this model. This result is supported by the contour curves (Figure 5), which indicate that adult female survival has a stronger impact than juvenile survival on population growth. The models where adult male harvest was varied showed that a higher proportion of males harvested resulted in an increase of total harvest (Figure 4 B and C). This is due to the lack of impact on population growth by removal of males.

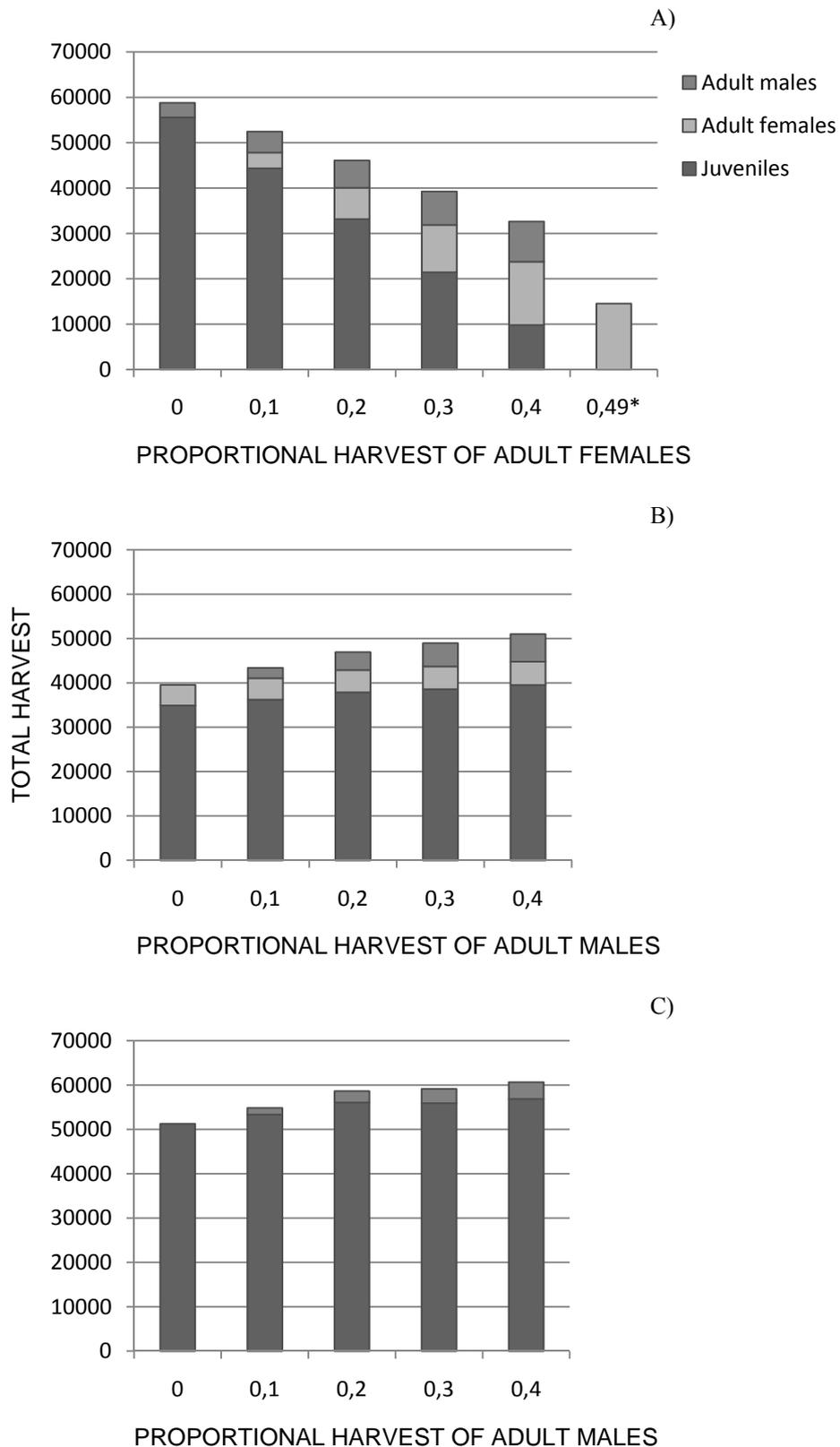


Figure 4. Examples of total number of harvested wild boar, given a population size of 150 000, depending on five management strategies which differs in A) the proportional harvest of juveniles and adult females, with harvest of adult males fixed at 0.3; B) the proportional harvest of juveniles and adult males, with harvest of adult females fixed at 0.15 and C) the proportional harvest of juveniles and males, with harvest of adult females fixed at 0.0.

\*Harvest of juveniles and adult males fixed at 0, harvest of adult females set at a level where population growth reaches  $\lambda \approx 1$

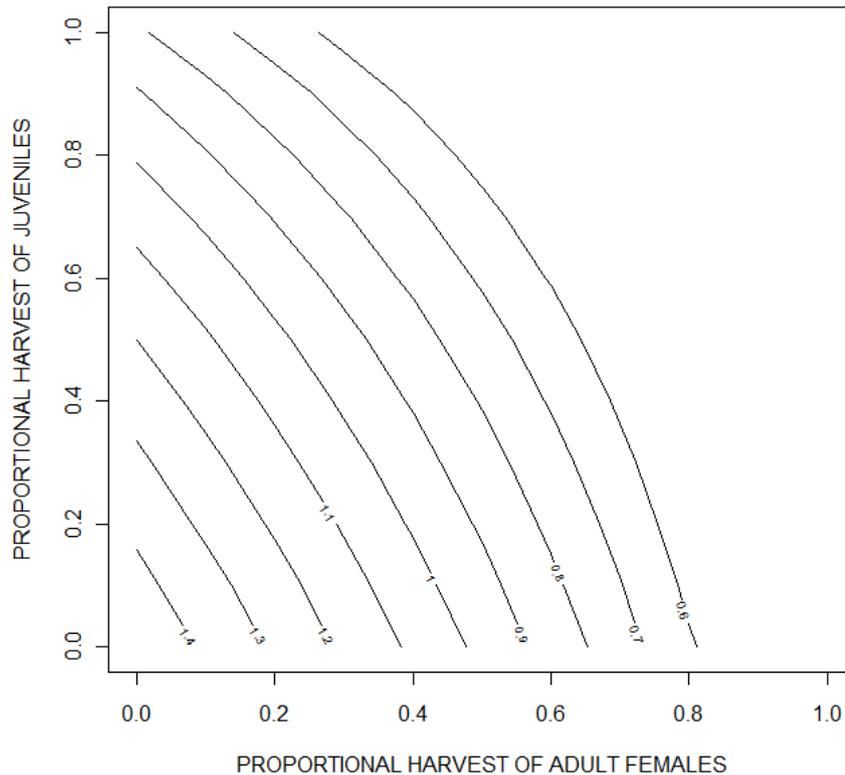


Figure 5. Population growth rate contour curves as a function of juvenile and adult female proportional harvest, for wild boar. These relations apply when the population has reached a stable sex- and age distribution during given proportional harvest.

## Discussion

The growth rate calculated from a projection matrix with data on vital rates from previous studies of wild boar was 1.48. This value is in the range of results from the study by Bieber & Ruf (2005), which is based on data from several other studies during various conditions and geographic locations. This growth rate indicates a potential mean annual increase in population size close to 50 % (assuming no hunting). With a random harvest strategy (where yearlings dominate the cull) and an initial population of 150 000 wild boar, this implies that a net increase of 72 000 animals needs to be harvested every year to keep a stable population. With an annual harvest of almost 50 000, as in 2009 (Jägareförbundet 2010b), i.e. ca 22 000 animals less than needed to keep the population stable, the population could still be more than doubled in 4 years (Table 4).

The elasticity of  $\lambda$  to vital rates was the greatest for juvenile survival and second greatest for adult survival (Table 2). This suggests that changes in these parameters have the strongest impact on population growth. The effect of varying harvest strategies on growth rate was further investigated by sex- and age structured models. These showed a substantially lowered total harvest by a higher proportional harvest of adult (>1 year) females. An increased proportional harvest of adult males instead increased the total harvest. These consequences are due to the change in population growth induced by a shift in population composition. The contour curves (Figure 5) also illustrate how the proportion of harvested adult females has a stronger impact on growth rate than the same proportion harvested juveniles.

### **Population growth rate - input data for the models**

The deterministic, density-independent model used here, gives the exponential growth under unlimited resources and non-variable conditions (Figure 3). This is a simplified projection of reality, because eventually the population would be limited by effects of density dependence. Competition for food may cause density dependence in birth and mortality rates (Melis et al. 2006), and in dense populations wild boar can be afflicted by diseases e.g. swine fever. Swine fever has not been detected in Sweden since 1944, but occurs in wild boar in several European countries (Jägareförbundet 2010a). However, the carrying capacity of the environment for wild boar is not known, and for the Swedish population the limitation may rather be determined by the tolerance of society/political decisions, which could be lower than that set by nature. This parameter is also influenced by seasonal variation in climate and, not the least, by effects of supplemental feeding.

More complex models are necessary to make the predictions more realistic, but sufficient data are not yet available. Data on vital rates under varying environmental conditions are lacking, and as in this study, the generality of data on reproduction and survival can be questioned. In Lemel's study (1999) recordings of actual litter sizes were not made, the sample size was small and the data on reproduction was collected in an area with supplemental feeding. When feeding is abundant, it should affect home ranges, population dynamics and food selection (Lemel 1999), but since feeding is common and probably will continue in Sweden, results from studies in areas where feeding occurs are still relevant. However, there is a lack of knowledge about correlations between vital rates and the amount of feeding, although it is likely that supplemental feeding promotes both survival and reproduction (Holmgren 2009).

Other investigations of population dynamics in wild boar agree that a deterministic model is not representative for a wild boar population. Environmental variability is necessary to incorporate to make the models realistic (Focardi et al. 1996, Náhlik & Sándor 2003, Bieber & Ruf 2005). The wild boar holds traits characteristic for r-strategic species, with reproductive and survival patterns closer to those expected for small mammals (Geisser & Reyer 2005, Focardi et al. 2008). The large capacity to increase in numbers during good conditions and the high mortality after e.g. severe winters, are the causes for the often observed large fluctuations in population sizes between years (Baskin & Danell 2003, Geisser & Reyer 2005). With this simple deterministic model, which doesn't cover any variability, the accuracy of the estimates of mean vital rates is important. Especially errors in rates which have a substantial effect on population growth may strongly affect the results.

### **Sensitivity & elasticity**

To answer the question of how a population responds to changes in one or several vital rates, elasticity analysis can be a helpful tool. It is considered to be a useful, fairly robust first step in investigations of population dynamics (Benton & Grant 1999, Mills et al. 1999). The vital rates that have the largest impact on growth rate can also be those which are most important to have good estimates for, in order to get accurate results from the models. This can be a guideline when deciding on which parameters should be prioritized in further field studies and management.

Since elasticity of  $\lambda$  were highest for survival of juveniles,  $e(P_1)$ , and adults,  $e(P_3)$  (Table 2), it could be interpreted as these parameters are most effective as tools for management. However, to be able to make a reliable interpretation of results from the sensitivity analysis, these should be investigated further, as exemplified by Mills et al. (1999). Small shifts in parameters will keep the elasticities valid, but with large-scale changes the matrix will reach a

new ranking of elasticities. This can be the case under strongly fluctuating conditions, as concluded by Bieber & Ruf (2005). Further, rates with low elasticity often tend to have a high variance, and thus in reality potentially a larger effect on population growth than rates with higher elasticity (Mills et al. 1999). For fecundities, the rankings of elasticity and sensitivity were reversed (Table 2). This is probably an effect of the age structure, where sensitivity reflects that the juvenile stage has a stronger effect by being great in numbers, while the proportional effect on growth is lower, as indicated by the elasticity. However, sensitivities are not suitable for comparing relative importance of vital rates to  $\lambda$ . This is because matrix entries can be proportional values, as for survival, or take larger values, as for litter sizes. Moreover, the values for fecundity also include survival probability.

It should be noted that the parameters are not equally possible to influence by management practices (De Kroon et al. 2000). Which parameters are the most easy/ethical/economic to manipulate may be an equally important aspect. If a parameter is rigid to change, elasticity will not tell us much about the effectiveness of the actions. Also, parameters do not always change independently of each other, which make the consequences more complex. Simultaneous changes in more than one parameter can further complicate the process, as for example here the added effect of  $e(P_2)$  and  $e(P_3)$  is 0.354, which is larger than  $e(P_1)$ . Sensitivity analysis of total models should be conducted in order to compare management strategies where more than one entry is changed. One way to accomplish this is presented by the above harvest models (Figure 4), which are more complex than the single-parameter based sensitivity.

### **Harvest simulations**

The results from the simple, non-structured model exemplify the magnitude of harvest volumes. Good knowledge about population size and the true rate of increase in the population is required to make the results accurate. Furthermore, it is not likely that harvest is random, i.e. that categories of animals are harvested relative to their proportion in the population at stable age distribution. This is because it is not equally possible to shoot different categories of wild boar due to hunting methods and difficulty to select eligible animals. If the selection is not random or the distribution not stable, these results will not apply in reality, since the sex- and age distribution and, consequently, the rate of increase will change. The population dynamics may also take unexpected routes due to stochastic effects. A fixed proportional harvest should settle the population at a stable density, even in the presence of environmental stochasticity. With the results from the non-structured model expressed as proportional harvest, a harvest of 32 % of the population after reproduction was needed for stability. However, to accomplish that in reality requires good annual estimates of population size, i.e. reliable census methods.

Unequal hunting pressure among different categories in the population result in other harvest levels than stated by the model discussed above, because sex- and age structure affects the growth rate. In the sex- and age structured harvest model here, the harvest was set to make the growth rate 1.0. The total harvest decreased with 45 % by an increased proportional harvest of adult females from 0.0 to 0.4 (Figure 4 A). With a population of 150 000 animals, the difference is 26 000, but for 250 000 and 350 000 the difference is 44 000 and 61 000, respectively. By increasing the proportional harvest of adult males, the result is a slightly increased total harvest compared to the example above. Increased harvest of adult males, i.e. lowered male density, does not affect growth rate much and thus, has little effect on population size.

Contour curves illustrate all possible combinations of proportional juvenile and adult female harvests to reach a given growth rate. The aimed growth rate applies when stable stage distribution for the current proportional harvest levels is reached. To lower the growth rate to 1.0 by harvest of only females, almost 50% of the female population needs to be removed. For a population of 150 000 this corresponds to 14 500 females. If only juveniles were harvested, nearly 80 % from this category needs to be removed every year, which results in 55 000 animals. Moreover, harvest of adult males only would, within reasonable numbers, not limit population growth, which leaves it on exponential growth. However, if the sex distribution gets extremely skewed, as when no females harvested (Figure 4 C), the lack of males would of course eventually affect population growth.

Especially at larger population sizes, the choice of harvest strategies can result in substantial differences in total harvest levels, as indicated by the examples above. The Swedish EPA stated in 2010 that the most effective way to slow down population growth in wild boar probably is very high hunting pressure on younger females during october-december (Anon. 2010a). My results also imply that this strategy would be the most effective. Moreover, high hunting pressure on adult females and piglets was advised also by other studies of wild boar population dynamics (e.g. Bieber & Ruf 2005, Toigo et al. 2007, Keuling 2010). However, there are many more aspects than the mathematical relationships that need to be considered. Models may be readily produced and even if their results would be correct to apply in real systems, some strategies may be difficult or even impossible to implement.

### **Management implications**

Selective harvest in accordance with a detailed plan (e.g. as the models above) encounters practical problems because of the difficulties with sex- and age determinations in the field (Jägareförbundet 2010a). This applies to both dominant hunting methods, i.e. beat/drive hunts where animals often get observed at great distances and/or in high speed, and still hunts (wait at selected sites often in full moon nights) due to poor light. Strategies including harvest of females, also call for ethical consideration, since culling of females obviously may result in motherless piglets. Besides that, is it also considered inappropriate to remove leading sows because that change the social structure in the family groups (Jägareförbundet 2010a, Keuling 2010), which may result in disrupted heat frequency, dispersal and establishment of new groups. Moreover, management strategies that state certain harvest levels per animal category, and if over-shooting would danger the system severely, also meet administrative obstacles. How should single hunters during the season be informed on what amount of animals that are still to be shot? Theoretically this could be solved by obligatory and frequent (e.g. weekly) reports to some administrative authority, e.g. the County board, but would involve quite a voluminous organization. Due to such difficulties to implement a strategy of intensified female harvest, the most attractive strategy for management is probably to aim for lowered juvenile survival. This however requires a high total harvest to keep the population in equilibrium.

The numbers presented for population density and bag per hunter (Table 3) are rough estimates, but interesting when compared to other game species. With 150 000 wild boars, population density was estimated to 13/1000 ha in the present distribution area. To shoot 0.38 wild boar per hunter (Table 3) may not look a lot, but the figure is in between the bag/hunter of moose (0.32) and roe deer (0.46) in the total of Sweden. Moose and roe deer are the most common game species in Sweden, and the comparison implies that quite an intense hunting effort is required to reach such levels. The mean harvest of wild boar per 1000 ha in the

focused region was 6.3 (total of 72 000), to compare to the moose harvest in the corresponding area between 0.6-3.8 per 1000 ha (varying among counties; Anon. 2009).

Although conventional hunting is the most important management tool to reduce population size (Geisser & Reyer 2004, Keuling 2010), the harvest effort needed may not be accomplished by voluntary hunters. If so, other methods of population control might be needed as a complement to hunting. In Sweden studies on trapping devices for wild boars are conducted at the moment (Naturvårdsverket 2009b). Intensive methods as aerial shooting, poisoning and trapping have been tried in other countries (Hone & Pedersen 1980, Hanson et al. 2009). However, besides ethical points of such methods, intensive efforts if not long-termed, can result in quick recovery due to compensatory reproductive response (Hanson et al. 2009) and increased immigration from neighboring areas.

Good food conditions, as generated by supplemental feeding, influence population growth by reducing juvenile mortality and strongly increase fertility and age of first reproduction (Okarma et al. 1995, Massei et al. 1997, Náhlik & Sándor 2003, Geisser & Reyer 2005, Keuling 2010). Thus, supplemental feeding has a great effect on population growth and enhances range expansion, since wild boars can survive almost anywhere with supplemental food available (Markström & Nyman 2002). Therefore, if official management aims to stabilize or decrease wild boar densities, restrictions of feeding activities may be necessary as concluded in several studies (e.g. Bieber & Ruf 2005, Geisser & Reyer 2005).

The choice of management strategy obviously depends on defined objectives. Strategies may include main- and subaims for e.g. population control (increase-stable-decrease), an attractive hunting, certain quality of the products (meat, trophies) etc. So far, no such aims (especially not quantified) are formulated at the national level in Sweden, which is unsatisfying to some stakeholders. Such official strategies are far from based on ecology solely, but constitute political decisions based on economy, public welfare etc. Aims for population size and composition, may also be based on pragmatic aspects, like what amount of animals the hunters likely manage to shoot yearly. Moreover, a recent study indicated that in counties with newly established wild boars, hunters preferred increased population density, whereas the attitude was the opposite in counties where they have been present for a longer period (Widemo et al. 2010). Furthermore, goals for population size should preferably be related to measures for damage mitigation along with methods to evaluate the results. At present, however, the relationship between local density and damage levels is unclear and suitable census methods are missing. Finally, population predictions on the national level may be relevant for various reasons, but for effective planning regional models would be even more useful, e.g. due to the often uneven abundance and varying environmental conditions also within limited regions (Anon. 2010a).

**Acknowledgements-** Most of all I thank my supervisor Gunnar Jansson, for your endless patience and for supporting and believing in me from beginning to end. I also thank Johan Månsson for guidance along the way and comments on my manuscript, and Guillaume Chapron for helpful advice. Per Grängstedt, I am glad you brought me along on exiting fieldwork, hunting and practice shooting when I was in urgent need to get away from the computer. I am also grateful to my family and friends who has been cheering on me all this time. Finally, I want to say thanks to everyone at Grimsö who have made my time here memorable and pleasant in so many ways!

## References

- Ahmad, E., Brooks, J.E., Hussain, I., Khan, M.H. 1995: Reproduction in Eurasian wild boar in central Punjab, Pakistan. - *Acta Theriologica*, 40(2): 163-173.
- Anonymous 2010a: Nationell förvaltningsplan för vildsvin *Sus scrofa* (In press). Naturvårdsverket. (In Swedish).
- Anonymous 2010b: Varg i Sverige vintern 2009/10 Preliminär statusrapport. Version 1.0. - Inventeringsrapport från Viltskadecenter 2010-2. (In Swedish). ISBN: 978-91-86331-16-0.
- Anonymous 2009: Årsrapport 2007-2008. - Svenska jägareförbundet, Viltforum nr 2. (In Swedish). ISBN: 978-91-88660-41-1.
- Anonymous 2008: Markanvändningen i Sverige, femte upplagan. (In Swedish with English summary: Land Use in Sweden, fifth edition. - Statistics Sweden). - Statistiska centralbyrån. ISBN: 978-91-618-1464-0.
- Anonymous 2007: Redovisning av regeringens uppdrag ifråga om förvaltning av vildsvin m.m. - Naturvårdsverket. (In Swedish). Dnr 412-5130-06.
- Anonymous 2006: Årsrapport 2005-2006. - Svenska jägareförbundet, Viltövervakningen. (In Swedish).
- Apollonio, M., Andersen, R. & Putman, R. 2010: Present status and future challenges for European ungulate management. - In: Apollonio, M., Andersen, R. & Putman, R. (Eds.); European ungulates and their management in the 21<sup>st</sup> century. University press, Cambridge 27: 578-604.
- Baskin, L.M. & Danell, K. 2003: Ecology of ungulates: a handbook of species in Eastern Europe and Northern and Central Asia. - Springer-Verlag Berlin, 434 pp.
- Benton, T.G. & Grant, A. 1999: Elasticity analysis as an important tool in evolutionary and population ecology. - *Trends in Ecology & Evolution* 14(12): 467-471.
- Bieber, C. & Ruf, T. 2005: Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. - *The Journal of applied ecology* 42(6): 1203-1213.
- Briedermann, L. 1990: Schwarzwild. - VEB Deutscher Landwirtschaftsverlag, Berlin, 540 pp.
- Brooks, E.N. & Lebreton, J.-D. 2001: Optimizing removals to control a metapopulation: application to the yellow legged herring gull (*Larus cachinnans*). - *Ecological Modelling* 136(2-3): 269-284.
- De Kroon, H., Van Groenendael, J. & Ehrlén, J. 2000: Elasticities: a review of methods and model limitations. - *Ecology* 81(3): 607-618.
- Focardi, S., Gaillard, J.-M., Ronchi, F. & Rossi, S. 2008: Survival of wild boars in a variable environment: unexpected life-history variation in an unusual ungulate. - *Journal of Mammalogy* 89(5): 1113-1123.
- Focardi, S., Toso, S. & Pecchioli, E. 1996: The population modelling of fallow deer and wild boar in a Mediterranean ecosystem. - *Forest Ecology and Management* 88: 7-14.
- Fransson, S. 1965: The borderland. - In: The plant cover of Sweden. *Acta Phytogeographica Suecica* 50: 167-175.
- Geisser, H. & Reyer, H.U. 2004: Efficacy of hunting, feeding, and fencing to reduce crop damage by wild boars. - *Journal of Wildlife Management* 68(4): 939-946.
- Geisser, H. & Reyer, H.U. 2005: The influence of food and temperature on population density of wild boar *Sus scrofa* in the Thurgau (Switzerland). - *Journal of Zoology* 267(01): 89-96.
- Goulding, M.J., Roper, T.J., Smith G.C. & Baker, S.J. 2003: Presence of free-living wild boar *Sus scrofa* in southern England. - *Wildlife Biology* 9 (Suppl. 1): 15-20.

- Hanson, L.B., Mitchell, M.S., Grand, J.B., Jolley, D.B., Sparklin, B.D. & Ditchkoff, S.S. 2009: Effect of experimental manipulation on survival and recruitment of feral pigs. - *Wildlife Research* 36: 185-191.
- Hauser, C.E., Cooch, E.G. & Lebreton, J.-D. 2006: Control of structured populations by harvest. - *Ecological Modelling* 196(3-4): 462-470.
- Herrero, J., García-Serrano, A. & García-González, R. 2008: Reproductive and demographic parameters in two Iberian wild boar *Sus scrofa* populations. - *Acta Theriologica* 53(4): 355-364.
- Holmgren, C. 2009: Hur mycket påverkar utfodring grisexplosionen? - *Jakt&Jägare* 3: 24-25. (In Swedish).
- Hone, J., Pedersen, H. 1980: Changes in a feral pig population after poisoning. - In: *Vertebrate Pest Conference Proceedings collection. Proceedings of the 9th Vertebrate Pest Conference, 1980. University of Nebraska, Lincoln.*
- Jansson, G., Månsson, J. & Magnusson, M. 2010: Hur många vildsvin finns det? - *Svensk Jakt* 4: 86-87. (In Swedish).
- Janulaitis, Z. 2003: Distribution, abundance and regulation of wild boar population in Lithuania. - *Acta Zoologica Lituonica* 13(1): 88.
- Jedrzejewska B., Jedrzejewski W., Bunevich A.N., Milkowski L. & Krasinski Z.A. 1997: Factors shaping population densities and increase rates of ungulates in Białowieża Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. - *Acta Theriologica* 42(4): 399-451.
- Keuling, O. 2009: Managing wild boar - Considerations for wild boar management based on game biology data. Grouping patterns, space use, dispersal, hunting impact, and hunting efficiency. - *Diss. Dresden University of Technology* 2010.
- Kratochvil, Z., Kux, Z. & Pikula, J. 1986: Age structure and reproduction of a population of *Sus scrofa* in Czechoslovakia. - *Folia Zoologica* 35(4): 311-324.
- Leaper, R., Massei, G., Gorman, M.L. & Aspinall, R. 1999: The feasibility of reintroducing wild boar (*Sus scrofa*) to Scotland. - *Mammal Review* 29(4): 239-259.
- Lemel, J. 1999: Populationstillväxt, dynamik och spridning hos vildsvinet, *Sus scrofa*, i mellersta Sverige. - Report, Swedish Environmental Protection Agency (In Swedish with English summary).
- Lemel, J. & Truvé J., 2008. Vildsvin, jakt och förvaltning - Kunskapssammanställning för LRF. - *Svensk Naturförvaltning AB. Rapport 04.*
- Markström, S. & Nyman, M. 2002: Vildsvin. - *Jägareförlaget/Svenska Jägareförbundet. Kristianstads Boktryckeri AB, Kristianstad.* (In Swedish).
- Massei, G., Genov, P.V., Staines, B.W. & Gorman, M.L. 1997: Factors influencing home range and activity of wild boar (*Sus scrofa*) in a Mediterranean coastal area. - *Journal of Zoology* 242(3): 411-423.
- Mattsson, L., Boman, M., Ericsson, G. 2008: Jakten i Sverige – Ekonomiska värden och attityder jaktåret 2005/06. - Rapport nr: 1 från Adaptiv förvaltning av vilt och fisk SLU Umeå. (In Swedish).
- Melis, C., Szafranska, P.A., Jedrzejewska, B. & Barton, K. 2006: Biogeographical variation in the population density of wild boar (*Sus scrofa*) in western Eurasia. - *Journal of Biogeography* 33:803-811.
- Mills, L.S., Doak, D.F. & Wisdom, M.J. 1999: Reliability of conservation actions based on elasticity analysis of matrix models. - *Conservation Biology* 13(4): 815-829.
- Moretti, M. 1995: Birth distribution, structure and dynamics of a hunted mountain population of wild boars (*Sus scrofa* L.), Ticino, Switzerland. - *Ibex J.M.E.* 3: 192-196.
- Náhlik, A. & Sándor, G. 2003: Birth rate and offspring survival in a free-ranging wild boar *Sus scrofa* population. - *Wildlife Biology* 9 (Suppl. 1): 37-42.

- Neet, C.R. 1995: Population dynamics and management of *Sus scrofa* in western Switzerland: a statistical modelling approach. - *Ibex J.M.E.* 3: 188–191.
- Okarma, H., Jedrzejewska, B., Jedrzejewski, W., Krasinski, Z.A., Milkowski, L. 1995: The roles of predation, snow cover, acorn crop, and man-related factors on ungulate mortality in Białowieża Primeval Forest, Poland. - *Acta Theriologica* 40(2): 197-217.
- Sáez-Royuela, C. & Tellería, J.L. 1986: The increased population of the wild boar (*Sus scrofa* L.) in Europe. - *Mammal Review* 16(2): 97–101.
- Toïgo, C. Servanty, S., Gaillard, J.-M., Brandt, S. & Baubet, E. 2008: Disentangling natural from hunting mortality in an intensively hunted wild boar population. - *Journal of Wildlife Management* 72(7): 1532–1539.
- Widemo, F., Ericsson, G., Bergström, R. & Kindberg, J. 2010: Jägarkårens attityder till vildsvinet som vilt (In press). - Fakta skog, SLU. (In Swedish).

### Internet

- Nationella viltolycksrådet 2010: Viltolycksstatistik väg år 2009. Available at: <http://www.viltolycka.se/upload/files/PreviousWebsite/Statistics/>, (Last accessed on 03 11 2010). (In Swedish).
- Jägareförbundet 2010a: Artpresentation – Vildsvin. Available at: <http://jagareforbundet.se/sv/Viltet/ViltVetande/Artpresentationer/Vildsvin/>, (Last accessed on 01 11 2010). (In Swedish).
- Jägareförbundet 2010b: Avskjutningsstatistik för svenska viltarter. Available at: <http://www.jagareforbundet.se/Viltet/Viltovervakningen/Avskjutningsstatistik/>, (Last accessed on 01 11 2010). (In Swedish).
- Naturvårdsverket 2010: Vildsvin i Sverige. Available at: <https://www.naturvardsverket.se:4545/sv/Arbete-med-naturvard/Jakt-och-viltvard/Vildsvin-i-Sverige/>, (Last accessed on 03 11 2010). (In Swedish).
- Naturvårdsverket 2009a: Riktlinjer för hjälpmedel vid vildsvinsjakt. Available at: <https://www.naturvardsverket.se:4545/sv/Arbete-med-naturvard/Jakt-och-viltvard/Vildsvin-i-Sverige/Riktlinjer-for-hjalpmedel-vid-vildsvinsjakt/>, (Last accessed on 03 11 2010). (In Swedish).
- Naturvårdsverket 2009b: Fälla för vildsvinsjakt. Available at: <https://www.naturvardsverket.se:4545/sv/Arbete-med-naturvard/Jakt-och-viltvard/Fallor-for-vilda-djur/Falla-for-vildsvinsjakt/>, (Last accessed on 08 11 2010). (In Swedish).

**Appendix I.** References for age-composition in wild boar populations.

- Ahmad et al. 1995  
Chegorka 1984 In: Baskin & Danell 2003  
Durov 1980 In: Baskin & Danell 2003  
Herrero et al. 2008  
Janulaitis 2003  
Jägareförbundet 2010a  
Moretti 1995  
Rusakov 1979 In: Baskin & Danell 2003  
Severtsov & Sablina 1953 In: Baskin & Danell 2003  
Sobansky 1992 In: Baskin & Danell 2003  
Sludsky 1956 In: Baskin & Danell 2003

**Appendix II.** Counties included in calculations for distribution area.

Stockholm  
Uppsala  
Södermanland  
Östergötland  
Jönköping  
Kronoberg  
Kalmar  
Gotland  
Blekinge  
Skåne  
Halland  
Västra Götaland  
Värmland  
Örebro  
Västmanland





Swedish University of Agricultural Sciences  
Faculty of Natural Resources and Agricultural Sciences  
Department of Ecology  
Grimsö Wildlife Research Station

