Master thesis:

The effect of the wolf (*Canis lupus*) on a potential outbreak of African Swine Fever in wild boar (*Sus scrofa*) in the Netherlands

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Abstract

In this master thesis I developed and explored a mathematical model to study the potential effect of the wolf (Canis lupus) on a hypothetical outbreak of African Swine Fever in wild boar (Sus scrofa) in the Netherlands (specifically the Veluwe). A deterministic mathematical SIR model was developed to simulate a wild boar population, African Swine Fever, infectious carcasses, and the predation behavior of wolves, allowing the exploration of different scenarios of control and intervention. Wolves and carcass transmission were found to have an effect on disease dynamics and control effort. The initial analyses show that the model has potential for more in-depth study and policy support, and it can be valuable to develop this further.

Introduction

African Swine Fever (ASF) has been a concern for many years in Europe. In January 2014 African Swine Fever (genotype II) was first discovered in Lithuania in wild boar. Since this discovery the pathogen seems to have shifted slowly more and more westward through wild boar populations. In 2020 ASF was discovered in wild boar at the German-Polish border (Sauter-Louis et al., 2021). Since 2020 multiple wild boars have been found infected with ASF in Germany (Friedrich Loeffler Institut, 2022). In July there was an outbreak in Germany close to the Dutch border (Emsbüren) in a sow farm (Ministerie van Landbouw, Natuur en Voedselkwaliteit, 2022). Between 2018 and 2020 there was also a contained outbreak of ASF among wild boar in Belgium. ASF was thought to be introduced by human activity (and thus not by the migration of boar). Strict biosecurity measures, including zoning, culling, fencing and carcass removal, were successfully implemented (Anette, et al., 2019). Belgium was declared ASF free in December 2020 by the OIE (Sauter-Louis et al., 2021).

The Netherlands is at the time of writing still ASF free, but there is a small, and possibly increasing, chance that ASF might be introduced from other countries at one point (Ministerie van Landbouw, 2020; Ministerie van Landbouw, Natuur en Voedselkwaliteit, 2022). Mur et al. (2014) found that importation of illegal pig products and transport-associated fomites form the highest risk factors for ASF introduction in the Netherlands (Mur et al., 2014). The Netherlands has a substantial pig industry. In 2021 it was estimated that more than 11 million pigs were kept for food production (Wageningen University & Research, 2022). Moreover, there are also three natural reserves ('the Veluwe', 'the Meinweg' and 'the Meerlebroek') designated to maintain populations of wild boar. Outside these designated areas wild boar populations do not have to be conserved. This means that they are either all culled ("zero wild boar policy") or managed by the Dutch provinces depending on the amount of damage they cause (Ministerie van Landbouw, 2020). Due to growing concerns regarding African Swine Fever and a growing wild boar population, the provinces of Limburg and Overijssel have increased efforts to reduce the population of wild boar outside of their designated areas. The provinces of Noord-Brabant and Gelderland maintain a strict zero wild boar policy outside the designated areas for wild boar. However, in some areas in Noord-Brabant this policy has proven hard to achieve and reduction efforts are in place (Provincie Noord-Brabant et al., 2022). Numbers of wild boar can increase rapidly if there is a high availability of food, which can make the population hard to maintain. In the summer of 2021, the number of wild boars in the Veluwe (one of the largest Dutch nature reserves) was very large compared to other years due to very good former mast years. The total number of wild boars was estimated to be 10.195 individuals. In 2019 this number was estimated to be 5671 individuals. The large increase in 2021 led the local provincial government to allow a relatively large number to be hunted that year (7690 individual boar) to bring the number eventually in line with the goal of around 1350 wild boar in the Veluwe. (Faunabeheereenheid Gelderland, 2022).

Wild boars in the Netherlands are regularly sampled for antibodies for ASF (Wageningen University & Research, z.d.). Due to the outbreak of ASF in a sow farm in Emsbüren (close to the Dutch border) in July 2022, the Dutch province of Overijssel is also sampling the carcasses of wild boar for ASF virus (Ministerie van Landbouw, Natuur en Voedselkwaliteit, 2022).

ASF transmission and mortality

African Swine Fever Virus is a DNA virus belonging to the family of *Asfarviridae* that causes symptoms in animals belonging to the family of *Suidae*. There are 24 known genotypes (Qu, et al., 2022). Genotype I is a less virulent variant that has caused outbreaks between the 1950's and 1980's in Europe. It has been eradicated except for Sardinia. Genotype II is the more virulent variant found in Eastern and Northern Europe today (Gaudreault et al., 2020). Symptoms of genotype II are mostly subacute to acute. They include epistaxis, melena, pulmonary distress, skin hemorrhages (petechia and ecchymosis), fever, anorexia and ataxia (Salguero, 2020; Sauter-Louis et al., 2021). Wild boars seem to lose fear of humans and dogs and can appear to be disorientated (Sauter-Louis et al., 2021). The most important pathological changes are hemorrhagic splenomegaly, multifocal hemorrhagic lymphadenitis and petechia on the kidney surface (Salguero, 2020). Most animals die within 7-14 days post infection, but some might recover (Sauter-Louis et al., 2021). Mortality is very high and is estimated to be around 90-100% for wild boar (Gaudreault et al., 2020; Salguero, 2020). It is speculated that mortality is higher in wild boar compared to domestic pigs (Salguero, 2020). A lot of wild boars have been found dead near water, which might mean that sick animals look for cool places as a reaction to their fever (Sauter-Louis et al., 2021). Transmission of the virus occurs through direct contact with blood, bodily fluids, feces or carcasses (including pork products) or through indirect contact through fomites (feed, clothes, uncleaned vehicles, equipment) or mechanic vectors (flies) (Gaudreault et al., 2020; Olesen et al., 2018). In Sub-Saharan Africa, transmission between wild warthogs also takes place through soft ticks. Eight species belonging to the *Ornithodoros* family have been found capable of transmitting ASFV to swine (Gaudreault et al., 2020). In Europe the *O. erraticus* tick has been found capable of transmitting ASFV and has been found to play a part in the transmission of ASF in the Iberian Peninsula. However, these ticks are largely absent in the colder climates of Northern and Eastern Europe. Therefore, it is thought that soft ticks do not play a (significant) part in the transmission of ASF in these regions (Gaudreault et al., 2020). The effect of transmission through mechanic vectors, like stable flies, is also thought to be negligible (Vergne, et al., 2020). Scavengers are also thought to play a negligible role in disease transmission (Probst et al., 2019). Moreover, wolves were not found to be able to transmit ASF through feces (Szewczyk et al., 2021). Infected carcasses though are thought to be very important in the transmission of ASF and might even be more important than direct transmission. Wild boars have been found to make direct contact with carcasses and there have even been accounts of cannibalism (Cukor et al., 2020; Probst et al., 2017). There are also recorded cases in the Netherlands of wild boar having contact with dead wild boar (Dooddoetleven, 2012; Dooddoetleven, 2013). The virus can persist in a carcass and the soil underneath for a substantial amount of time depending on the tissue, temperature and soil type. This can vary from days for soils, like beach sand and yard soil, to over a year for blood (at 4 °C) (Probst et al., 2017; Sauter-Louis et al., 2021).

The wolf

In 2015 the first wolf was sighted in the Netherlands since the 19th century when it had become extinct (Natuurmonumenten, n.d.). In 2018 the first new wolf territory was established in the Netherlands and in 2019 the first wolf couple was formed, and the first pups were born. In 2022 it was estimated that there were four wolf couples living in the Netherlands and at least 16 wolf pups were born in the areas of Zuidwest-Drenthe/Zuidoost-Fryslân, Noord-Veluwe, Midden-Veluwe and Park de Hoge Veluwe. (BIJ12, 2022) The wolf is a tightly protected species under CITES (International), the Convention of Bern (European Union) and the Habitats Directive (Council Directive 92/43/EEC; European Union). In the Netherlands 'de Wet Natuurbescherming' forms the legal framework for the protection of the wolf (Interprovinciaal overleg, 2019). The growth of wolf populations lies around 25-36% per year depending on the area and is expected to decrease when most suitable habitats are occupied. In Germany the initial growth rate between 2000-2015 was 36% and decreased several years later to 26%. In the US the growth rate of the wolf population is 25% (Jansman et al., 2021). There seems to be agreement that the wolf population in the Netherlands will grow. However, how large the population will become is still unclear. Leliveld (2012) estimated that there would be a carrying capacity for a minimum of 14 wolf packs in the Netherlands. Potiek et al. (2012) found a carrying capacity in the Netherlands with a maximum of 338-443 wolves (68-89 wolf packs).

The wolf is a very opportunistic carnivore and diet can vary according to prey availability. In Europe the most important prey species are wild boar (*Sus scrofa*), roe deer (*Capreolus capreolus*), chamois (*Rupicapra rupicapra*), moose (*Alces alces*) and red deer (*Cervus elaphus*). Depending on the location, livestock can form either an absent, a small or large part of the diet of the wolf. (Klich et al., 2021; Lanszki et al., 2011; Newsome et al., 2016; Wagner et al., 2012; Žunna et al., 2009) In Germany wild boar contributed to 17,7% of the diet of the wolf. Other important prey species for German wolves were roe deer (55,3%) and red deer (20,8%) (Wagner et al., 2012). However, if prey populations drop, the wolf easily starts consuming other prey. A case study in Belarus found that wolves that first hunted mainly elk and wild boar started hunting other prey, like beavers and deer, when the population of wild boar dropped due to an ASF outbreak (Kitch et al., 2021). Moreover, a recent study found that wolves on Pleasant Island (United States) started hunting otters, after the number of deer on the island declined (Roffler et al., 2023)

(Top) predators, like the wolf, are thought to play an important role in maintaining healthy ecosystems, like aiding carbon storage, enhancing scavenger diversity and reducing stream bank erosion (Ripple et al., 2014). Predators also play an important role in reducing numbers of prey animals. Areas without wolves for example were found to have a 6x higher number of cervids compared to areas with wolves (Ripple et al., 2014). Moreover, predators might be able to reduce disease burdens in prey populations. This is not only achieved by decreasing the density of prey animals, but also through the selection of weaker (infected) animals when hunting (Gehman, &, Beyers, 2017; Genovart et al., 2010; Krumm et al., 2009; Ripple et al., 2014). Selection of diseased animals during hunting has also been observed in wolves (Mech & Peterson, 2003/2006a). Several mathematical models have also found that predators could reduce disease prevalence in prey species (Hall et al., 2005; Packer et al., 2003; Al-Shorbaji, et al., 2017). The loss of (top) predators has in some cases even been linked to an increase in (zoonotic) diseases (Ostfeld, &, Holt, 2004; Levi et al., 2012). In North America for example, the loss of top predators might have allowed the population of coyotes to grow, which in turn caused numbers of small predators like foxes to decline. This might have caused an increase in small vertebrates and thus in the prevalence of Lyme disease (Levi et al., 2012).

As the diet of the wolf contains a substantial amount of wild boar and scavenged meat, the wolf might influence the disease dynamics of ASF in wild boar populations. Szewczyk et al. (2021) already speculated that scavenging by wolves could play an important role in reducing ASF transmission. Moreover, Tanner et al. (2019) showed through a mathematical model that the wolf might be able to reduce tuberculosis prevalence in wild boar in Spain through predation of infected individuals. However, in the case of ASF, the wolf might also have the potential to increase the prevalence of disease. As wolves do not always eat a whole prey in one sitting, they can increase the number of carcasses and lengthen the time that a killed infected wild boar remains infectious in the environment (Wilmers et al., 2003). Carcasses play an important role in the transmission of the disease and therefore an increase in carcasses might cause an increase in ASF.

Modelling ASF in wild boar

We cannot do experiments to assess the effects of different interventions and control measures on an outbreak of ASF in wild boar in the Netherlands, nor to assess the potential influence of the wolf. The complexity of interactions in the ecosystem and feedback mechanisms that act on it, notably through human intervention, make it very difficult or impossible to regard population consequences in the short and long term of ASF in this system and scenarios of response. Mathematical models are a useful tool to include key aspects of the complex system and to then perform scenario analysis (“what if”). Several mathematical models have already been constructed to simulate the transmission of ASF in wild boar populations in several settings. These have mainly been focused on comparing intervention methods or country-specific situations (Croft et al., 2020; Halasa et al., 2019; Lange, 2015; Lange et al., 2017; Lange et al., 2018; O’Neill et al., 2020). Intervention measures that have been modeled include removal of carcasses, culling, buffer zones and fences. Removing carcasses was found to be the most effective intervention method in these studies (Lange, 2015; Lange et al., 2018; O’Neill et al., 2020). However, Croft et al. (2020) found that carcass removal did not reduce outbreak length when modelling an ASF outbreak in an isolated wild boar population in the Forest of Dean (UK).

To the author's knowledge no model has yet considered the influence of the wolf in the setting described above. Here, I investigate this for the Dutch situation (with a focus on the Veluwe) and investigate the effect of the wolf on the prevalence of ASF in wild boar. As the Netherlands is a country with both a large pig industry and substantial populations of wild boar, a mathematical model might add valuable epidemiological information regarding ASF. Moreover, in the increasingly polarized debate about the wolf in the Netherlands, providing information based on scientific analysis on either the benefits or disadvantages of this predator to the Dutch ecosystem is important (NOS, 2022). In this master thesis an outbreak of ASF in the wild boar population and the effectiveness of several intervention methods will be modeled. Moreover, the effect of the wolf on ASF prevalence in the wild boar population will be assessed.

Material & Methods

A mathematical model was constructed to simulate the wild boar population, African swine fever genotype II and predation by wolves for different scenarios in the Netherlands. The model conforms to a compartmental, deterministic SIR-model (Diekmann et al., 2013). The mathematical model was adapted from an ASF model from O'Neill, et al., 2020. Wild boars are divided in two age classes: Piglets (P) and adults (A). Each age class is further divided in either susceptible (S), infected (I) or recovered (C). The division in two age classes allows for the modelling of distinct population dynamics for piglets and adults. This is especially important regarding the mortality and birth rates and predation. In addition to these compartments of living animals, we also regard the infected carcasses as a separate compartment (D). A schematic representation of the model is given in Figure 1.

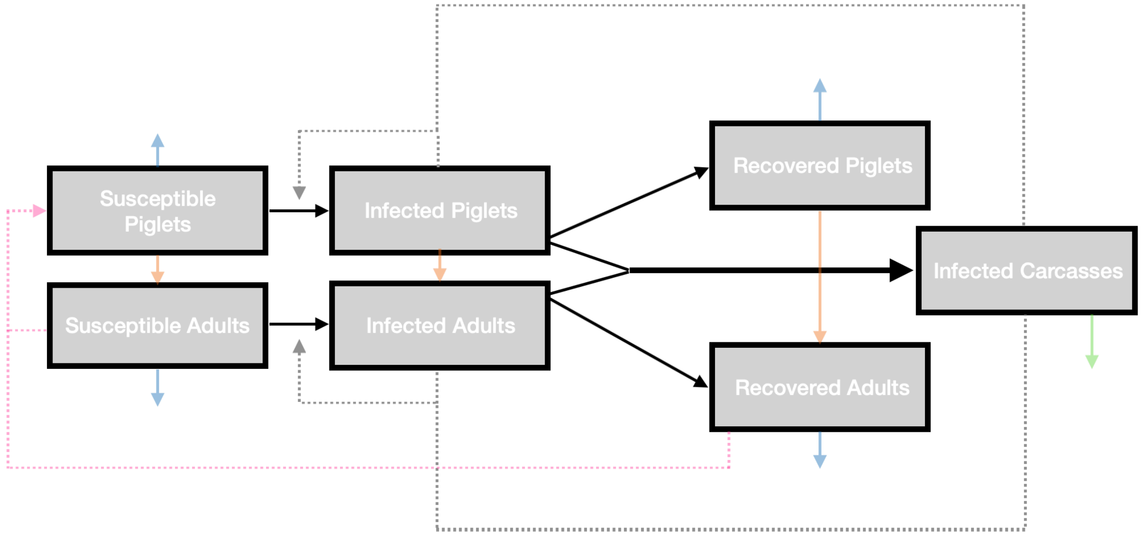


Figure 1: Schematic presentation of the SIR model. The pink line denotes births, the grey lines the infection routes, the blue line denotes background mortality and the orange line denotes maturation.

Susceptible individuals

Piglets are born with a rate of *a*. As it is still unknown if piglets attain maternal immunity and the proportion of surviving animals is generally very small, all newborn piglets are added to the susceptible population. On average a sow gives birth to 5.5 piglets a year (5.5/365 piglets a day) and there are on average 1.4 adult females for every male. (Pascual-Rico et al., 2022) It is thus assumed that 71,4% of the adult population is always female. Moreover, only susceptible and recovered females reproduce and infected sows do not. Infected animals recover or die relatively fast (after 14 days) and symptoms can be very severe (Sauter-Louis et al., 2021). This makes the likelihood of an infected animal giving birth very small. The number of piglets born per day is therefore calculated as $a^*(S_A + C_A)$. Piglets are assumed to move to the adult compartment at one year old. For convenience, this is modeled with an exponential distribution, with maturation rate α = 1/365 per day, whereas in reality, piglets remain in the piglet compartment for the entire year.

Infectious individuals

Transmission between susceptible and infectious animals is assumed to be density dependent (Diekmann et al., 2013). Transmission through direct contact happens at a rate β_F (written as ‘BetaF’ in text and figures below). The transmission rate after contact with carcasses (β_E, written as ‘BetaE’ in text and figures below) is assumed to be frequency dependent (Diekmann et al., 2013). If an animal from either of the infected compartments dies, it moves to the (infected) carcass compartment (D).

Recovered individuals

Animals enter the recovered compartment at rate $\gamma(1-\rho)$, in which γ denotes the rate of losing infectivity (i.e., $1/\gamma$ is the average number of days that an animal is infectious with ASF). Animals leaving the infectious compartment can do so in two ways. They can die as a result of the infection, which we consider happening with probability ρ, or they can recover, with the complementary probability $1 - \rho$. Recovered animals are assumed to be immune, although it is still unknown if immunity develops in wild boar after infection and the number of animals surviving is generally very small (Sauter-Louis et al., 2021).

Carrying capacity

To stop endless exponential growth, a carrying capacity (*H*) was added. The carrying capacity was linked to the ideal population size wildlife management at the Veluwe tries to maintain (around 1300 animals) (Faunabeheereenheid Gelderland, 2022). To achieve this, the background hunting rate (b_h) was made dependent on the difference between the ideal population size (*K*) and the actual population size (*N*). It was assumed that each animal above the ideal population size would increase the background hunting rate with 1% per year. This is represented by *x* in the following formula:

$$H = b_h + x^*(N - K)$$

If an infected animal is hunted it is assumed to be removed from the environment in a bio-secure manner, and therefore these animals will not flow to compartment D.

Carcasses

Animals enter compartment D with a rate of *γρ*. The degradation rate of the carcasses *d*(*t*) is considered to change according to season due to changes in temperature. The weight of the animal is not considered to play a role in the degradation rate. Based on German measurements, the degradation rate in winter was thought to be on average 37 days and in summer 8 days (Probst et al., 2019). Seasonal changes in the degradation rate were therefore calculated as:

$$d(t) = \frac{1}{22{,}5 + 14{,}5 * cos(2 * \pi * \frac{t}{365})}$$

In this formula the lowest degradation rate of 37 days corresponds to the 1st of January and the highest degradation rate of 8 days corresponds to June 30th.

Interventions

The model includes three different causes of mortality: Background mortality (with rate b_P), culling (b_C) and predation by wolves (b_W). The background mortality consists of the average yearly hunting rate in a disease-free population for population management, traffic mortality, and death through natural causes (e.g., old age, other diseases, interspecies fighting). Culling is considered an intervention method that can be deployed in case of an ASF outbreak and that consists of the systematical killing of a large amount of wild boar on top of the regular management. It is assumed that hunters do not make a distinction in the health and age of wild boar. Predation is dependent on the number of wolves and independent from the number of wild boars. On average a wolf eats 2,8 kg of meat a day and 17,7% of this diet consists of wild boar (based on German literature) (Szewczyk et al., 2021; Wagner et al., 2012). The weight of a piglet is on average 34,4 kg, of an adult 65,0 kg and the average weight of all age classes of wild boar combined is 47,5 kg (Pascual-Rico et al., 2022). With this data the average amount of wild boar an individual wolf is expected to eat per day can be calculated:

$$b_{W_P} = \frac{(2{,}8 * 0{,}177 * \frac{1}{3})}{34{,}4}$$

$$b_{W_A} = \frac{(2{,}8 * 0{,}177 * \frac{1}{3})}{65{,}0}$$

$$b_{W_D} = \frac{(2{,}8 * 0{,}177 * \frac{1}{3})}{47{,}5}$$

The constant *q* in the compartment of infected denotes a change in the preference of the wolf for infected wild boar. It is assumed that a carcass only gets partially eaten after a wolf kills an infected boar. Therefore, infected animals that are killed by wolves are first transported to compartment D instead of being removed from the system altogether. The parameter *r* denotes the carcass removal rate per day by human intervention in case of an outbreak, in which all carcasses that are found are removed as a bio-security measure.

In the model, the population of wolves is assumed to be of constant size *W*. In the analyses, a range of values for *W* is assessed. As the wild boar is only a small part of the diet of a wolf, the wolf's dynamics are not heavily dependent on the dynamics of the wild boar. In addition, the wolf can easily switch its prey preference.

The total population of wild boar is $N = S + I + C$. The total number of infected individuals is $I = I_p + I_A$ and the total number of adults through $A = S_A + I_A + C_A$. All in all, the above assumptions lead to the following system of ordinary differential equations:

$$\frac{dS_p}{dt} = 0.7a - \beta_F \frac{S_p}{N} I - \beta_E S_p D - \alpha S_p - b_p S_p - b_C S_p - b_W W$$

$$\frac{dS_A}{dt} = -\beta_F \frac{S_A}{N} I - \beta_E S_A D + \alpha S_P - b_A S_A - b_C S_A - b_W W$$

$$\frac{dI_p}{dt} = \beta_F \frac{S_p}{N} I + \beta_E S_p D - \alpha I_p - \gamma I_p - b_p I_p - b_C I_p - q b_W W$$

$$\frac{dI_A}{dt} = \beta_F \frac{S_A}{N} I + \beta_E S_A D + \alpha I_P - \gamma I_A - b_A I_A - b_C I_A - q b_W W$$

$$\frac{dC_p}{dt} = \gamma(1-\rho) I_p - \alpha C_p - b_p C_p - b_C C_p - b_W W$$

$$\frac{dC_A}{dt} = \gamma(1-\rho) I_A + \alpha C_p - b_A C_A - b_C C_A - b_W W$$

$$\frac{dD}{dt} = \gamma \rho I + b_P I_P + b_A I_A + q b_W I_p W + q b_W I_p W - d(t) D - rD - b_W W$$

Table 1: Parameters

Symbol	**Meaning**	**Values**	**Source**
$S_{P\text{ (start)}}$	Susceptible piglets	456	Faunabeheereenheid Gelderland, 2022
$S_{A\text{ (start)}}$	Susceptible adults	844	Faunabeheereenheid Gelderland, 2022
$I_{P\text{ (start)}}$	Infected piglets	0	
$I_{A\text{ (start)}}$	Infected adults	0	
$C_{P\text{ (start)}}$	Immune piglets	0	
$C_{A\text{ (start)}}$	Immune adults	0	
$D_{\text{ (start)}}$	Infected carcasses	0	
a	Births	0,011	Pascual-Rico et al., 2022
β_F	Transmission rate	0.007143	Lange, 2015
β_E	Carcass transmission rate	0.0286	Lange, 2015
α	Maturation	1/365	
b_p	Background mortality of piglets	-log(0.9957)	Keuling et al., 2013
b_A	Background mortality of adults	-log(0.9988)	Keuling et al., 2013
b_h	Hunting rate	0.56/365	Pascual-Rico et al., 2022
bc	Culing rate	0-0,9	
b_{WP}	Proportion of piglets killed per wolf per day	0,0048 boar/wolf/day	Pascual-Rico et al., 2022; Szewczyk et al., 2021; Wagner et al., 2012
b_{WA}	Proportion of adults killed per wolf per day	0,0025 boar/wolf/day	Pascual-Rico et al., 2022; Szewczyk et al., 2021; Wagner et al., 2012
b_{WD}	Proportion of carcasses eaten by the wolf	0,0035 boar/wolf/day	Pascual-Rico et al., 2022; Szewczyk et al., 2021
q	Preference of the wolf for infected boar	1	
d	Carcass degradation rate	1/8 (summer); 1/37 (winter)	Probst et al., 2019
r	Carcass removal rate	0-0,9	
ρ	Mortality of ASF	0,95	Gaudreault et al., 2020; Salguero, 2020
γ	Average number of days that a boar is infectious with ASF	1/14	Sauter-Louis et al., 2021
W	Number of wolves	0-300	
t	Time in days	0-3650	
K	Ideal population size	1300	Faunabeheereenheid Gelderland, 2022
H	Carrying capacity	~	

Computed scenarios

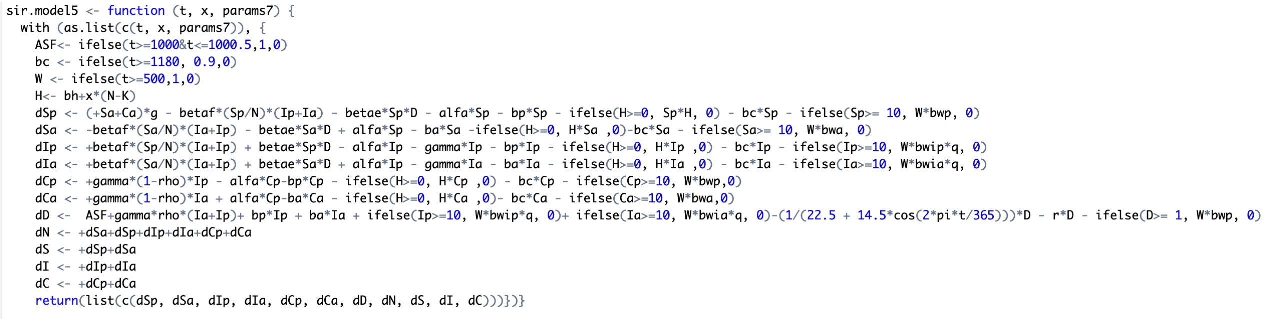
For the above model the following five scenarios were computed:

Table 2: The modeled scenarios

	Carcass removal	Culling	Wolf
Scenario 1			
Scenario 2	x		
Scenario 3		x	
Scenario 4			x
Scenario 5	x	x	
Scenario 6		x	x
Scenario 7	x		x
Scenario 8	x	x	x

Two additional scenarios without ASF were also simulated: one without the wolf and one with the wolf.

R studio (version 2022.12.0+353) was used for all calculations with the model (see Figure 2). To make R studio suitable for running an SIR model, the deSolve package was installed.



```
sir.model5 <- function (t, x, params7) {
  with (as.list(c(t, x, params7)), {
    ASF<- ifelse(t>=1000&t<=1000.5,1,0)
    bc <- ifelse(t>=1180, 0.9,0)
    W <- ifelse(t>=500,1,0)
    H<- bh+x*(N-K)
    dSp <- (+Sa+Ca)*g - betaf*(Sp/N)*(Ip+Ia) - betae*Sp*D - alfa*Sp - bp*Sp - ifelse(H>=0, Sp*H, 0) - bc*Sp - ifelse(Sp>= 10, W*bwp, 0)
    dSa <- -betaf*(Sa/N)*(Ia+Ip) - betae*Sa*D + alfa*Sp - ba*Sa -ifelse(H>=0, H*Sa ,0)-bc*Sa - ifelse(Sa>= 10, W*bwa, 0)
    dIp <- +betaf*(Sp/N)*(Ia+Ip) + betae*Sp*D - alfa*Ip - gamma*Ip - bp*Ip - ifelse(H>=0, H*Ip ,0) - bc*Ip - ifelse(Ip>=10, W*bwip*q, 0)
    dIa <- +betaf*(Sa/N)*(Ia+Ip) + betae*Sa*D + alfa*Ip - gamma*Ia - ba*Ia - ifelse(H>=0, H*Ia ,0) - bc*Ia - ifelse(Ia>=10, W*bwia*q, 0)
    dCp <- +gamma*(1-rho)*Ip - alfa*Cp-bp*Cp - ifelse(H>=0, H*Cp ,0) - bc*Cp - ifelse(Cp>=10, W*bwp,0)
    dCa <- +gamma*(1-rho)*Ia + alfa*Cp-ba*Ca - ifelse(H>=0, H*Ca ,0)- bc*Ca - ifelse(Ca>=10, W*bwa,0)
    dD <-  ASF+gamma*rho*(Ia+Ip)+ bp*Ip + ba*Ia + ifelse(Ip>=10, W*bwip*q, 0)+ ifelse(Ia>=10, W*bwia*q, 0)-(1/(22.5 + 14.5*cos(2*pi*t/365)))*D - r*D - ifelse(D>= 1, W*bwp, 0)
    dN <- +dSa+dSp+dIp+dIa+dCp+dCa
    dS <- +dSp+dSa
    dI <- +dIp+dIa
    dC <- +dCp+dCa
    return(list(c(dSp, dSa, dIp, dIa, dCp, dCa, dD, dN, dS, dI, dC)))})}
```

Figure 2: A screenshot of the implementation of the model in R Studio

A few additional rules were required for the ordinary differential equations. Based on the case report of Klitch et al. (2021), it was assumed that if the population of a compartment fell under 10 animals, the wolf would stop hunting wild boar and switch to other prey species. As the wolf might still find and eat a carcass of an infected wild boar this was not assumed for carcasses. However, as the chance that a wolf finds a carcass will also decrease if there are only small numbers of carcasses in the environment, it was assumed that the wolf would stop eating carcasses if there is less than one carcass present in the environment. Moreover, this was also done to prevent the wolf from eating more carcasses than there are present in the environment, causing D to become negative. This was achieved through the following code:

```
ifelse(Ip>=10, W*bwip, 0)

ifelse(D>= 1, W*bwp, 0)
```

In *ifelse(Ip>=10, W*bwip, 0)*, *Ip* was replaced for *Sa, Sp, Ia, Ca* or *Cp* depending on the compartment to which the code applied. The same was done for *bwip*. If the code applied to an infected compartment the parameter *q* was added to the code.

The variables *W, ASF, bc* and *r* were integrated in the model at a certain time point through the following code:

```
ASF<- ifelse(t>=1000&t<=1000.5,1, 0)

W <- ifelse(t>=500, x, 0)
```

The *x* in the function of *W* corresponds with the number of wolves that are introduced at time point *t*.

The results that R Studio produced were collected, sorted and analyzed in several Excel files.

Results

In total ten scenarios were investigated with the model. The disease dynamics were assessed through graphs and through quantifying the maximum and minimum number of infected, the minimum population size and the maximum and minimum number of carcasses.

Scenario without the wolf and ASF

Without the wolf and an ASF outbreak the model reached a population that corroborates with the aspired population in the Veluwe of around 1300 wild boars (Faunabeheereenheid Gelderland, 2022). The equilibrium was reached at around 1320 wild boars after 400 days (see Figure 3).

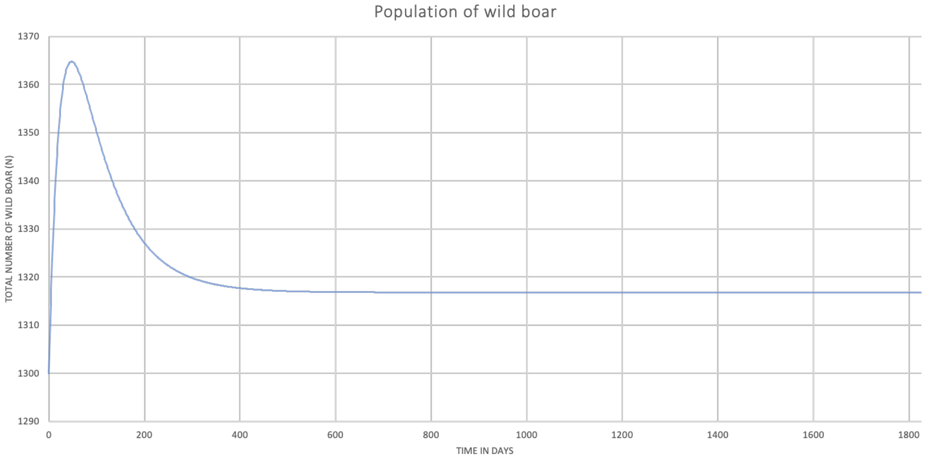


Figure 3: The population of wild boar over time without ASF or wolves

Scenario with wolf and without ASF

Different numbers of wolves were introduced in the model on day 500. Due to predation of the wolf the number of wild boars in the new equilibrium was lower when a larger number of wolves was introduced (see Figure 4). When 300 wolves were introduced, the equilibrium settled around 1260 wild boars. The apparently small effect of a large number of wolves on the population of wild boar, might have to do with the coupling of the background hunting rate to the carrying capacity: This rate goes down if the population of wild boar falls beneath the carrying capacity. Hunting will therefore cause less mortality, compensating for the mortality caused by the wolf.

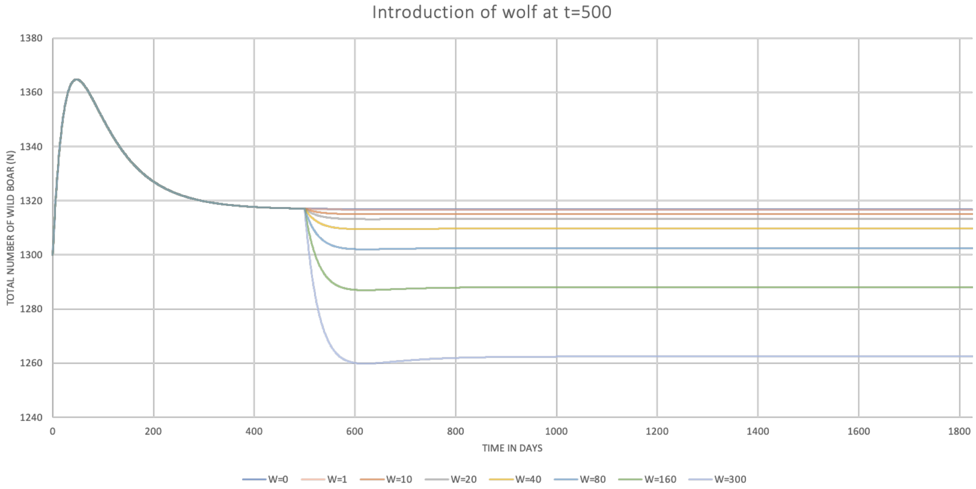


Figure 4: The population of wild boar over time after different numbers of wolves are introduced on day 500.

Scenario 1: Introduction of ASF

ASF was introduced on day 1000 and the outbreak was modeled until 3650 days. The carcass transmission rate (BetaE) was found to have a large effect on the course of the outbreak (see Figure 5). The initial outbreak lasts longer if the carcass transmission rate is lower. Moreover, the peak number of infected and carcasses is lower for a smaller carcass transmission rate. The number of wild boars that stay present after the initial outbreak is also higher for a lower carcass transmission rate.

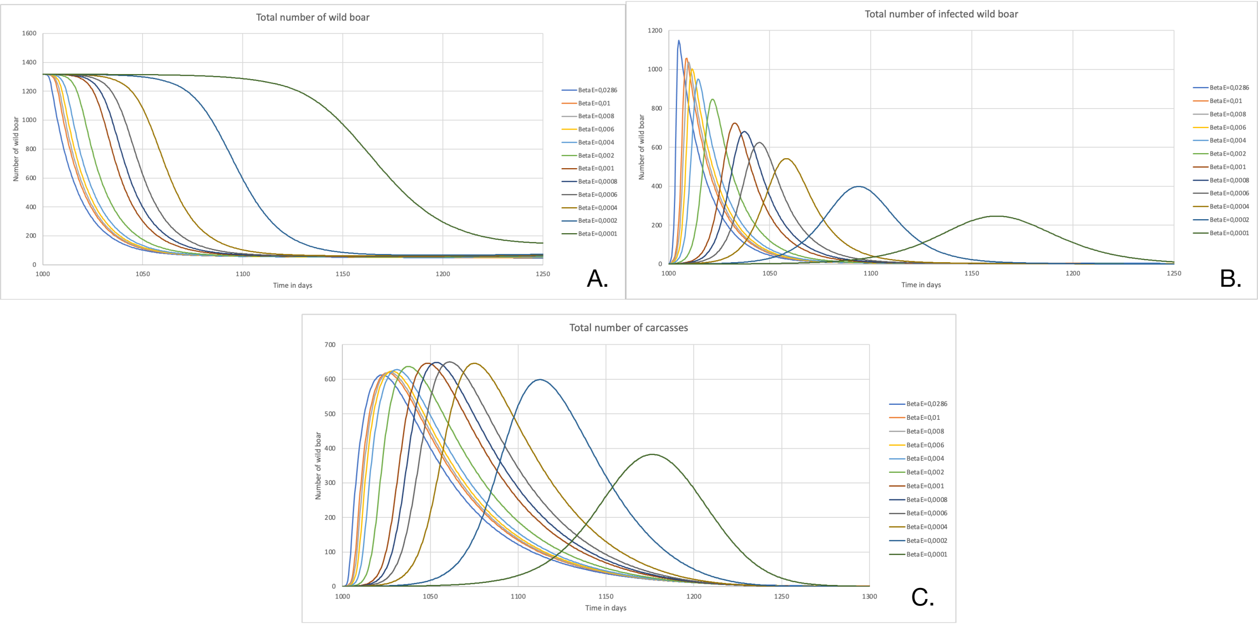


Figure 5: The course of the disease after ASF is introduced at a 1000 days for different carcass transmission rates (BetaE). **A**.: The total population of wild boar; **B**.: The number of infected; **C**. The number of carcasses

Carcass transmission rates higher than 0,001 seem to eventually lead to extinction of the population of wild boar or a non-viable population size. For a carcass transmission rate of 0,002 for example the infection dies out and there are six susceptible (of which four are piglets) and five recovered boars remaining after 3409 days (see Table 3). As can be seen in Figure 6 this number seems to keep decreasing overall.

Table 3: Smallest population size for different carcass transmission rates (BetaE)

	Total population	**Susceptible population**	**Number of suscepible adults**	**Number of susceptible piglets**	**Infected population**	**Number of infected adults**	**Number of infected piglets**	**Recovered population**	**Number of recovered adults**	**Number of recovered piglets**	**Number of carcasses**	***Time in days***
BetaE=0,0286	5,0820188	0,6033034	0,0458155	0,5574879	0,7079875	0,115106	0,5928816	3,7707279	3,4998961	0,2708318	2,3017756	*3650*
BetaE=0,01	7,1725103	1,6961379	0,1772014	1,5189365	0,5058408	0,0907271	0,4151136	4,9705316	4,5912976	0,379234	1,5258272	*3397*
BetaE=0,008	8,2130215	2,8345809	0,5085594	2,3260215	0,4968241	0,1300548	0,3667693	4,8816166	4,5090071	0,3726095	0,8588688	*3428,5*
BetaE=0,006	11,050585	3,3564001	0,5094559	2,8469442	0,7033508	0,1647178	0,5386331	6,9908339	6,4545302	0,5363037	1,487729	*3054*
BetaE=0,004	11,919334	6,096351	1,6603761	4,4359749	0,5560396	0,1891809	0,3668587	5,2669434	4,8348544	0,4320891	0,8332686	*3434*
BetaE=0,002	13,188822	5,7897628	1,455291	4,3344718	0,6543431	0,2185316	0,4358115	6,7447161	5,9337725	0,8109436	2,158786	*3409*
BetaE=0,001	25,093389	9,8301602	2,3453007	7,4848595	1,2871561	0,4570107	0,8301453	13,976072	11,912508	2,0635641	3,7630069	*2695*
BetaE=0,0008	35,297179	21,706535	7,2149361	14,491598	1,3926054	0,5479132	0,8446922	12,198039	10,711139	1,4869001	3,009889	*3054,5*
BetaE=0,0006	53,740683	26,518325	7,865285	18,65304	2,4440783	0,995964	1,4481142	24,77828	21,156297	3,6219826	3,3794937	*1991,5*
BetaE=0,0004	40,333794	9,9836287	1,3602064	8,6234223	2,2496288	0,5733084	1,6763205	28,100537	22,356107	5,7444296	25,311869	*2278*
BetaE=0,0002	53,130238	10,713475	0,6708003	10,042675	3,0555479	0,6766951	2,3788528	53,130238	66,899261	17,621259	61,020014	*1196*
BetaE=0,0001	147,00136	89,54244	33,778063	55,764377	4,6939938	2,3126916	2,3813022	52,764926	35,553977	17,210949	7,1986751	*1266,5*

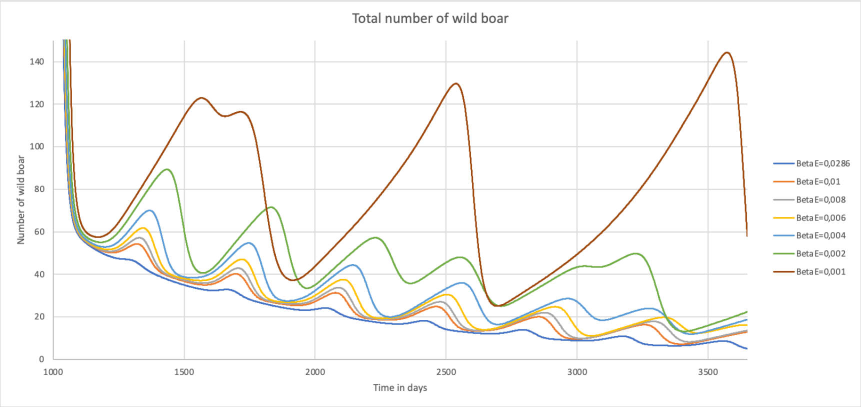


Figure 6: The population of wild boar for carcass transmission rates of 0,001 and lower.

A carcass transmission rate of less than 0,0006 was found to cause the number of carcasses and infected to decrease to very small amounts in the course of the outbreak. A carcass infection rate of 0,0004 for example lead the number of carcasses to decrease to 6,54E-06 and the number of infected to 4,77E-06 at 2816 days (see Table 4). These numbers correlate to extinction of the disease. However, the nature of a deterministic model, makes that the infection never fully disappears and therefore can cause new outbreaks (see Annex 1, Figure II).

Table 4: Smallest number of carcasses between 1000 and 3650 days for different carcass transmission rates (BetaE)

	Number of carcasses	**Infected population**	**Number of infected adults**	**Number of infected piglets**	**Total population**	***Time in days***
BetaE=0,0286	0,08273900	0,118288488	0,0191929	0,0990956	7,7994526	*3496,5*
BetaE=0,01	0,01335056	0,011800238	0,0026632	0,0091371	10,014160	*3531*
BetaE=0,008	0,02024528	0,015865766	0,0040516	0,0118141	10,727310	*3540*
BetaE=0,006	0,02244784	0,018003948	0,0043704	0,0136336	14,836803	*3173*
BetaE=0,004	0,02037591	0,013412726	0,0044173	0,0089954	15,326732	*3554*
BetaE=0,002	0,00262796	0,001143216	0,0003858	0,0007574	20,244975	*3602*
BetaE=0,001	0,00045280	0,000452134	0,0001957	0,0002565	67,925400	*3158*
BetaE=0,0008	0,00312902	0,003435957	0,0015640	0,0018720	88,999211	*3516,5*
BetaE=0,0006	0,00943727	0,004929375	0,0013037	0,0036257	94,413776	*1386,5*
BetaE=0,0004	0,00000654	4,76742E-06	2,07543E-06	2,6920E-06	126,72276	*2816*
BetaE=0,0002	0,00000127	1,27E-06	5,9949E-07	6,6552E-07	382,36031	*2049*
BetaE=0,0001	0,00002421	2,7668E-05	1,33973E-05	1,4271E-05	699,14381	*2054*

In the field often one large first outbreak, diminishing 85-95% of the population, is observed followed by an endemic phase (O'Neill et al., 2020). Although, further analyses would be needed to distinguish if a carcass transmission ration of 0,0006 and 0,0008 or a ratio in between would be more suited, it was decided to use a carcass transmission rate of 0,0008 for the modelling of the scenarios 5, 6 and 7. Due to the time constraint of this thesis further analysis of the carcass transmission ratio and the modelling of 3 to 4 different variables in scenarios 5, 6 and 7 was not possible.

Scenario 2: The effect of carcass removal during an ASF outbreak

The effect of carcass removal was modeled for a carcass removal rate of 0,01 to 0,9 in 18 steps (0,01, 0,02 … 0,1, 0,2, …) for 10 different carcass transmission rates and introduction at three different time points (1014, 1030 and 1180). This resulted in 540 different outbreak scenarios.

For a carcass transmission rate of 0,0008, the time at which carcass removal started lead to different disease dynamics. If carcass removal was started at 14 days after the introduction of infection, the peak number of infected and of carcasses decreases compared to a situation without carcass removal. The population of wild boar will decrease less dramatically if more carcasses per day are removed. However, the outbreak will also last longer if the carcass removal rate is higher. This might be due to less animals animals being infected per time unit due to a lower number of carcasses. Therefore, there is a less significant population crash and there are more susceptible animals present in the environment. The combination of more susceptible animals and less carcasses, causes the outbreak to last longer.

If carcasses are starting to be removed 30 days after introduction of ASF, the peak number of infected wild boar and carcasses decreases compared to a situation without carcass removal. However, unlike when carcass removal would be initiated at day 1014, the duration of the outbreak does not last longer. The number of carcasses also falls earlier if more carcasses are removed each day. The total population decreases less steeply if a higher carcass removal rate is present. For a carcass removal rate of 0,8 there seems to be an equilibrium. This equilibrium breaks at after 2500 days (see Annex 2, Figure III). However, this is probably due to the deterministic nature of the model, as the number of carcasses has already decreased to 4,05E-07 after 1675 days and the number of infected animals has decreased far below 1 at that point (see Table 5 and Annex 2, Table V).

When carcass removal is initiated at day 1180, there is mostly an effect on the population size. The population grows back to a higher level, if a higher carcass removal rate is implemented. If there is a carcass removal rate of 0,2 or higher, the population even grows back to a level similar to that before the outbreak (see Figure 7, A3.). However, the removal of carcasses has no effect on the peak number of infected or the length of the initial outbreak. It has a relatively small effect on the fall in the number of carcasses at the end of the initial outbreak (see Figure 7, C3.).

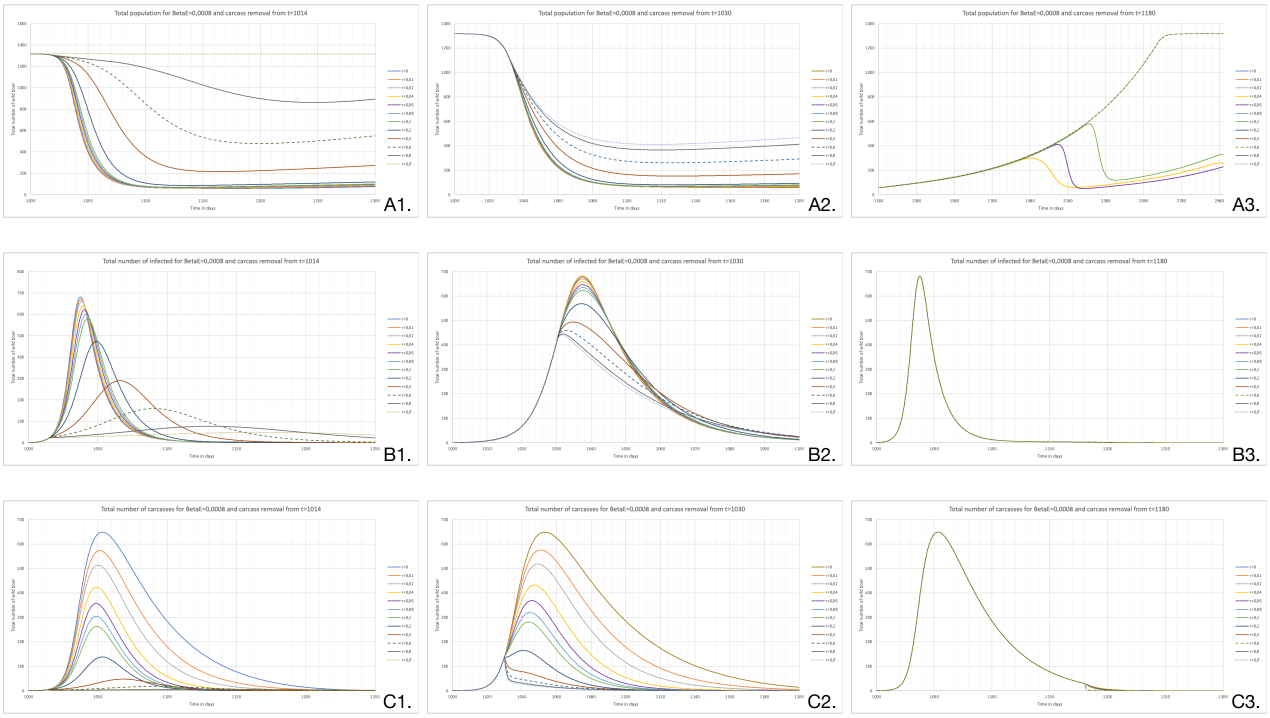


Figure 7: The course of the disease after ASF is introduced at a 1000 days for different carcass removal rates (*r*) and a carcass transmission rate (*BetaE*) of 0,0008. **A**.: The total population wild boar for carcass removal initiated at day 1014 (*A1.*), day 1030 (*A2.*) and day 1180 (*A3.*). Note that the graphic of *A3.* starts at 1180 days and not 1000 days.; **B**.: The number of infected for carcass removal initiated at day 1014 (*B1.*), day 1030 (*B2.*) and day 1180 (*B3.*); **C**. The number of carcasses for carcass removal initiated at day 1014 (*C1.*), day 1030 (*C2.*) and day 1180 (*C3.*)

In all outbreak scenarios related to carcass removal, the population of wild boar never falls below 31 animals (see Table 5). In the case that carcass removal is started at 14 or 30 days after introduction of the disease, i.e., on day 1014 or 1030, respectively, the minimal number of animals even seems to grow consistently with a higher carcass removal rate.

Table 5: Smallest population size for different carcass removal rates and different starting times of removal (BetaE=0,0008)

	Total population (removal started at t=1014)	***Time in days***	**Total population (removal started at t=1030)**	***Time in days***	**Total population (removal started at t=1180)**	***Time in days***
No carcass removal	35,297179	*3054,5*	35,297179	*3054,5*	35,297179	*3054,5*
r= 0,01	31,2255913	*2991,5*	31,1632165	*2991*	32,1766489	*2998*
r= 0,02	35,3026394	*2979*	35,1465382	*2978,5*	45,2358197	*3438,5*
r= 0,03	60,1754491	*1991*	59,9852778	*1991*	58,3981253	*1169,5*
r= 0,04	65,4750731	*1130,5*	65,3643856	*1129*	58,3981253	*1169,5*
r= 0,05	58,3108292	*3011*	58,9416304	*3011*	39,1485495	*3370*
r= 0,06	65,8851427	*2200,5*	66,1168061	*2200*	49,3621082	*3437,5*
r= 0,07	48,4195548	*3366,5*	48,3907879	*3366*	54,9985361	*2304,5*
r= 0,08	56,9710073	*3427,5*	57,0709832	*3428,5*	58,3981253	*1169,5*
r= 0,09	62,0727841	*2282,5*	61,8854905	*2282*	58,3981253	*1169,5*
r= 0,1	67,3557841	*2312*	67,134942	*2312,5*	58,3981253	*1169,5*
r= 0,2	86,7117301	*1136,5*	81,2806196	*1125*	58,3981253	*1169,5*
r= 0,3	133,611405	*1149,5*	109,396091	*1127*	58,3981253	*1169,5*
r= 0,4	216,031547	*1163,5*	152,791232	*1128*	58,3981253	*1169,5*
r= 0,5	332,010522	*1180*	205,292146	*1127,5*	58,3982335	*1169,5*
r= 0,6	478,80462	*1199*	260,986789	*1125,5*	58,3982335	*1169,5*
r= 0,7	655,039213	*1222*	315,518981	*1122,5*	58,3982335	*1169,5*
r= 0,8	862,693889	*1247*	366,220947	*1119,5*	58,3982335	*1169,5*
r= 0,9	1111,35607	*1268*	411,828589	*1116,5*	58,3982335	*1169,5*

If carcass removal is started at day 1030 or 1180, the number of carcasses (and infected animals) falls far below a number necessary to maintain transmission of ASF. This is achieved with the removal of at least 3 to 4% of carcasses per day (see Table 6). If the removal of carcasses starts two weeks after the introduction of ASF, a higher carcass removal rate (starting from 40% per day) seems to increase the smallest number of carcasses that is present in the environment between 1001 and 3650 days. This might be due to the less dramatic drop of the population size and thus the presence of more susceptible animals that can be infected. This eventually causes several small and long-lasting outbreaks (see Annex 2, Figure III). Not enough carcasses are present in the environment due to their daily removal to infect a large enough population to cause a substantial outbreak and crash in the population size. However, more analyses should be done to discover the mechanisms behind this.

Table 6: Smallest number of carcasses for different carcass removal rates and different starting times of removal (BetaE=0,0008)

	Number of carcasses (removal started at t=1014)	***Time in days***	**Number of carcasses (removal started at t=1030)**	***Time in days***	**Number of carcasses (removal started at t=1180)**	***Time in days***
No carcass removal	0,00312902	*3516,5*	0,00312902	*3516,5*	0,00312902	*3516,5*
r= 0,01	4,1633E-05	*3525,5*	4,0539E-05	*3525,5*	6,2302E-05	*3524,5*
r= 0,02	2,0524E-05	*3524*	1,9204E-05	*3524*	0,00342217	*1403,5*
r= 0,03	0,00108994	*1396*	0,00108099	*1395,5*	0,00087606	*1672*
r= 0,04	0,00038324	*1414*	0,00037718	*1413,5*	0,00012943	*1677,5*
r= 0,05	0,00010585	*1667*	0,00010609	*1667*	6,6782E-06	*2784*
r= 0,06	1,9163E-05	*1671,5*	1,902E-05	*1671*	9,4484E-07	*2799*
r= 0,07	3,0179E-06	*2781,5*	3,0114E-06	*2781,5*	8,5456E-07	*2810,5*
r= 0,08	5,0452E-07	*2796*	4,8493E-07	*2796*	2,1364E-07	*1706*
r= 0,09	2,3974E-07	*1686*	2,2292E-07	*1685,5*	5,6272E-08	*1716*
r= 0,1	7,2009E-08	*1692*	6,4343E-08	*1691,5*	1,6102E-08	*1727,5*
r= 0,2	2,8678E-10	*1757,5*	5,9807E-11	*1771,5*	1,5184E-13	*2036,5*
r= 0,3	6,0715E-09	*1738*	5,1338E-11	*1796,5*	-7,596E-13	*2297*
r= 0,4	1,7767E-06	*1682*	6,0343E-10	*1766,5*	-9,705E-13	*2334,5*
r= 0,5	0,00038384	*1630*	7,869E-09	*1730*	-2,932E-16	*2813*
r= 0,6	0,01110544	*1475*	5,5413E-08	*1703,5*	-1,637E-15	*2944,5*
r= 0,7	0,10009069	*1424,5*	1,9902E-07	*1686*	-5,602E-06	*3650*
r= 0,8	0,46210095	*1393,5*	4,0472E-07	*1675,5*	-3,435E-15	*3115*
r= 0,9	0,49206108	*1001*	5,2906E-07	*1670,5*	-3,548E-15	*2732,5*

The time to extinction decreases between a carcass removal rate of 0,04 and 0,1, if it is assumed that an amount of 0,001 carcasses or less would be unlikely to transmit ASF (see Table 7). If carcass removal starts at 14 days after introduction of ASF, a carcass removal rate of 0,6 or higher would prevent the disease from dying out. If carcasses would be removed from day 1180 onward, the time to extinction decreases when there is a higher carcass removal rate.

Table 7: Time at which the number of carcasses fall below 0,001

	Number of carcasses (removal started at t=1014)	***Time in days***	**Number of carcasses (removal started at t=1030)**	***Time in days***	**Number of carcasses (removal started at t=1180)**	***Time in days***
r= 0,01	0,00099708	*2397,5*	0,0009964	*2397*	0,00099904	*3386*
r= 0,02	0,00099878	*2384*	0,00099198	*2383,5*	-	-
r= 0,03	-	-	-	-	0,00099563	*1651*
r= 0,04	0,00099953	*1325,5*	0,00099823	*1324,5*	0,00099384	*1373*
r= 0,05	0,00098635	*1303*	0,00099553	*1301,5*	0,00098999	*1349*
r= 0,06	0,00098015	*1289*	0,00097773	*1287,5*	0,00099726	*1335*
r= 0,07	0,00098724	*1279*	0,0009909	*1277*	0,00099489	*1325,5*
r= 0,08	0,00099921	*1271,5*	0,00097752	*1269,5*	0,00098503	*1318,5*
r= 0,09	0,00099667	*1266*	0,00097152	*1263,5*	0,00099701	*1312,5*
r= 0,1	0,00098087	*1262*	0,0009768	*1258,5*	0,0009888	*1308*
r= 0,2	0,00097677	*1255,5*	0,0009895	*1241*	0,00099207	*1285*
r= 0,3	0,00098301	*1280*	0,00097482	*1246*	0,00096791	*1276*
r= 0,4	0,00099779	*1327*	0,00099317	*1255,5*	0,0009892	*1270*
r= 0,5	0,0009977	*1430*	0,00098599	*1265,5*	0,00098665	*1266*
r= 0,6	-	-	0,00098125	*1273,5*	0,00097782	*1263*
r= 0,7	-	-	0,00098165	*1278,5*	0,00097431	*1260,5*
r= 0,8	-	-	0,00099713	*1280*	0,00099872	*1258*
r= 0,9	-	-	0,00098357	*1279,5*	0,00097331	*1256,5*

Scenario 3: The effect of culling during an ASF outbreak

The effect of culling was modeled similar to the carcass removal rate. The culling rate consisted out of 18 steps (0,01, 0,02 … 0,1, 0,2, …) for 10 different carcass transmission rates and introduction of ASF at 3 different time points (day 1014, 1030 and 1180). This resulted in 540 different outbreak scenarios.

If culling would be initiated at day 1014 or day 1030, the peak number of infected and carcasses will be reduced, and the outbreak will be shorter (see Figure 8). If culling would start at day 1180 it could prevent new outbreaks from occurring. However, it has no effect on the peak number of infected and carcasses or duration of the initial outbreak.

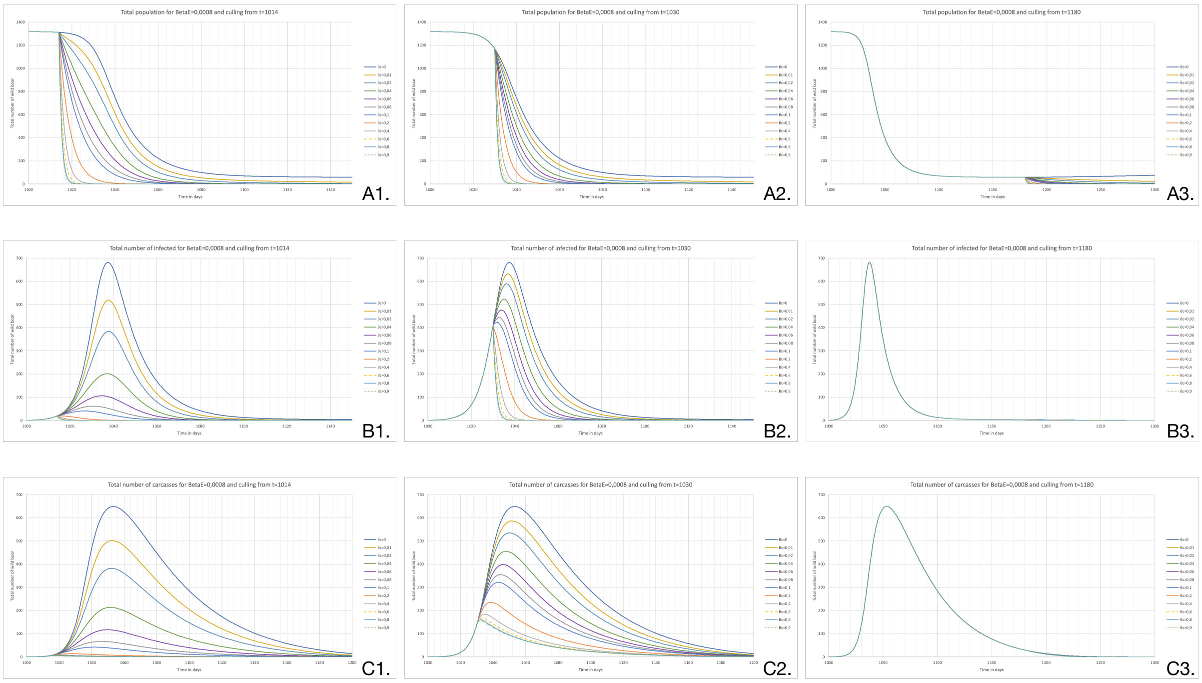


Figure 8: The course of the disease after ASF is introduced at a 1000 days for different culling rates (*Bc*) and a carcass transmission rate (*BetaE*) of 0,0008. **A**.: The total population wild boar for culling from day 1014 (*A1.*), day 1030 (*A2.*) and day 1180 (*A3.*).; **B**.: The number of infected for culling from day 1014 (*B1.*), day 1030 (*B2.*) and day 1180 (*B3.*); **C**. The number of carcasses for culling from day 1014 (*C1.*), day 1030 (*C2.*) and day 1180 (*C3.*)

For all culling rates ASF and the population of wild boar become extinct. If culling is started at day 1014 the population would fall below 1 at day 1495 for a culling rate of 0,01 and at day 1022 for a culling rate of 0,9. Under the assumption that if the number of carcasses falls below 0,001, ASF would be extinct, a culling rate of 0,01 would make ASF extinct at day 1305 and a culling rate or 0,9 would make ASF extinct at day 1240. If culling starts at day 1030, the population falls below 1 at day 1512 for a culling rate of 0,01 and at day 1038 for a culling rate of 0,9. ASF is extinct at day 1308 for a culling rate of 0,01 and at day 1274 for a culling rate of 0,9. Culling from day 1180 onward causes the population to fall below 1 at day 1697 when the culling rate is 0,01 and at day 1185 when the culling rate is 0,9. ASF becomes extinct at day 1358 when the culling rate is 0,01 and at day 1297 when the culling rate is 0,9. Overall, the earlier culling is initiated, the earlier ASF and the wild boar population will become extinct.

Scenario 4: The effect of the wolf during an ASF outbreak

The effect of the wolf was modeled for 1 to 300 wolves, starting with 1 wolf to 10, 20 and then increasing the amount with 20 with each step (16 steps in total). The carcass transmission ratio was varied from 0,0286 to 0,0001 in 12 steps. This led to 192 different outbreak dynamics. In general, the outbreak occurs later and the peak number of infected is lower, if the number of wolves is higher (see Figure 9).

For a carcass transmission rate of 0,0008 and 220 wolves, there seems to be an equilibrium (see Figure 9 and Annex 4, Figure V). The number of carcasses never exceeds 1,00 and the population size stays above 1244 individuals. This equilibrium might be due to the wolves eating enough carcasses to prevent a large number of wild boars from getting infected, but not eating so many live wild boars that the population size decreases. When there are more than 220 wolves, the population size might decrease through the mortality in wild boar being higher than the number of births due to the added mortality of ASF and a large number of wolves. However, calculations have to be interpreted with caution due to R Studio having difficulties to solve differential equations numerically, and due to continuity issues arising from the code *ifelse(D>= 1, W*bwp, 0)* that makes wolves stop eating carcasses when they fall below 1. A sign that the latter could be the cause is that the number of carcasses never exceeds 1,00. For a number of wolves larger than 220 the number of carcasses also stays around 0,99 for a long time until the number of carcasses eventually crashes (for 300 wolves this is around 2260 days, for 280 wolves around 2450 days and for 260 wolves around 2730 days). The crash might be due to a smaller population leading to a smaller number of wild boars being infected. The number of carcasses does not grow beyond 1 and therefore ASF is eventually unable to sustain itself in the population. However, more analyses with a more sophisticated solver of systems of nonlinear differential equations should be done to investigate these issues and clarify whether or not the behavior around 220 wolves is an artifact of the calculations.

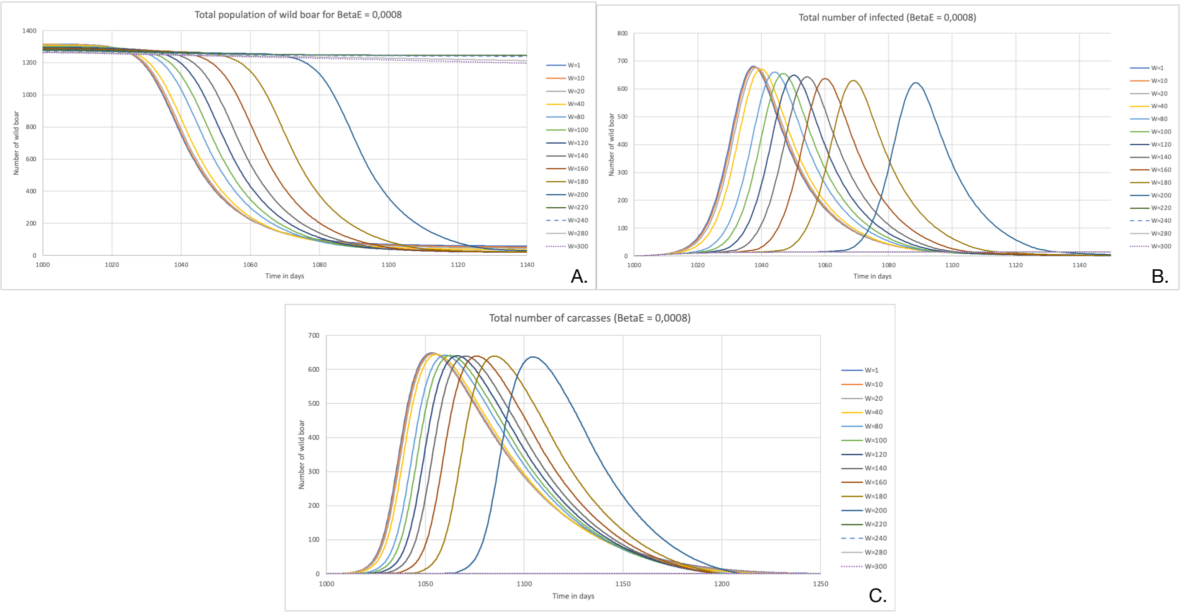


Figure 9: The course of the initial ASF outbreak for different numbers of wolves (*W*) and a carcass transmission rate (*BetaE*) of 0,0008.; **A**.: The total population wild boar.; **B**.: The total number of infected.; **C**. The total number of carcasses.

The population of wild boar does not go extinct, even for higher numbers of wolves, although the number of wild boars can get relatively small (see Table 8). The lowest number of wild boars seems to settle at 20 wild boars for most numbers of wolves. As mentioned earlier, 220 wolves seem to be the exception due to an equilibrium that causes the number of wild boars not to fall below 1244.

Table 8: Lowest number of wild boar for different numbers of wolves and BetaE=0,0008

	Total population	**Susceptible population**	**Number of suscepible adults**	**Number of susceptible piglets**	**Infected population**	**Number of infected adults**	**Number of infected piglets**	**Recovered population**	**Number of recovered adults**	**Number of recovered piglets**	**Number of carcasses**	***Time in days***
No wolves	35,297179	21,706535	7,2149361	14,491598	1,3926054	0,5479132	0,8446922	12,198039	10,711139	1,4869001	3,009889	*3054,5*
1 wolf	19,9581272	6,35441164	1,14781826	5,20659338	0,99580623	0,27101786	0,72478837	12,6079093	10,2386539	2,36925541	9,21096976	*3002*
10 wolves	38,6475536	28,8922131	11,5334445	17,3587686	0,35694388	0,17471218	0,1822317	9,39839669	7,76298742	1,63540927	0,37703402	*2404*
20 wolves	20,7418926	19,9998335	9,9999151	9,99991843	-4,084E-13	1,278E-28	1,1244E-28	0,7420591	0,74205887	2,2566E-07	8,8316E-28	*3650*
40 wolves	20,6686958	19,9999107	9,9999382	9,99997245	-7,031E-12	4,0066E-30	3,5252E-30	0,66878518	0,668785	1,8522E-07	2,7679E-29	*3650*
60 wolves	20,1562962	3,87952785	0,24670106	3,63282679	0,7496683	0,08108682	0,66858148	15,5271	9,9997026	5,52739744	9,46431211	*1193*
80 wolves	19,1664442	2,68113948	0,1316335	2,54950598	0,75712343	0,08056314	0,67656029	15,7281813	9,99975332	5,72842797	16,5614321	*1182*
100 wolves	19,0326314	2,42365776	0,10712789	2,31652987	0,75627463	0,08170605	0,67456858	15,852699	9,99978375	5,85291528	19,1938118	*1178,5*
120 wolves	19,0219889	2,34335505	0,09977263	2,24358242	0,75820611	0,08452116	0,67368495	15,9204278	9,99956592	5,92086185	19,6379306	*1178*
140 wolves	19,0421497	2,30262109	0,09584931	2,20677179	0,75777662	0,08801999	0,66975663	15,981752	9,99987216	5,9818798	19,2950532	*1179*
160 wolves	19,0845435	2,27288408	0,09275681	2,18012727	0,75635632	0,09268823	0,66366809	16,0553031	9,99986007	6,05544301	18,5872873	*1181,5*
180 wolves	19,1653172	2,28049354	0,09213706	2,18835648	0,74287794	0,09847804	0,6443999	16,1419458	9,99995127	6,14199449	16,6797595	*1187*
200 wolves	19,4024607	2,34053166	0,09426694	2,24626472	0,71666104	0,11642127	0,60023978	16,345268	9,99984552	6,34542244	12,4789774	*1200,5*
220 wolves	1244,34333	1216,21839	573,807834	642,410553	14,4701781	7,24535517	7,22482295	13,6547671	9,99922516	3,65554192	1,00015465	*2611,5*
240 wolves	27,3819973	19,9997535	9,99991385	9,99983967	0,00078377	0,00041711	0,00036666	7,38145996	7,23851465	0,14294531	0,00294408	*3650*
260 wolves	23,3679787	19,9998485	9,99994582	9,99990269	1,3302E-10	7,1884E-11	6,3224E-11	3,36813017	3,36660675	0,00152342	5,0169E-10	*3650*
280 wolves	22,3028046	19,9997305	9,99988489	9,99984558	-1,418E-12	2,7637E-14	2,431E-14	2,30307415	2,30290715	0,000167	1,9217E-13	*3650*
300 wolves	21,7910679	19,9998362	9,99997634	9,99985981	-2,045E-12	1,2193E-17	1,0726E-17	1,79123178	1,79119545	3,6327E-05	8,4618E-17	*3650*

In contrast with a situation with no wolves, all numbers of wolves seem to cause an eventual extinction of ASF in the wild boar population and carcasses at a certain point with exception of

220 and 240 wolves (see Table 9). However, at 240 wolves the number of carcasses might further decline after 3650 days as is observed at 260, 280 and 300 wolves.

Table 9: Lowest number of carcasses for different numbers of wolves and BetaE=0,0008

	Number of carcasses	**Infected population**	**Number of infected adults**	**Number of infected piglets**	**Total population**	***Time in days***
No wolves	0,00312902	0,003435957	0,0015640	0,0018720	88,999211	*3516,5*
1 wolf	2,0064E-06	1,3754E-06	6,0584E-07	7,696E-07	59,5025775	*3551*
10 wolves	4,4166E-05	3,6358E-05	1,7523E-05	1,8835E-05	65,4891549	*3172*
20 wolves	8,8316E-28	-4,084E-13	1,278E-28	1,1244E-28	20,7418926	*3650*
40 wolves	2,7679E-29	-7,031E-12	4,0066E-30	3,5252E-30	20,6686958	*3650*
60 wolves	1,0659E-29	2,2683E-13	1,5429E-30	1,3575E-30	20,657179	*3650*
80 wolves	7,0659E-30	-1,06E-12	1,0229E-30	8,9996E-31	20,6526952	*3650*
100 wolves	6,0265E-30	5,5301E-13	8,724E-31	7,6758E-31	20,652233	*3650*
120 wolves	5,5331E-30	-1,74E-12	8,0096E-31	7,0473E-31	20,6527976	*3650*
140 wolves	5,2941E-30	2,0334E-13	7,6636E-31	6,7428E-31	20,6546579	*3650*
160 wolves	5,2942E-30	-3,097E-12	7,6636E-31	6,7429E-31	20,6577172	*3650*
180 wolves	5,6933E-30	-5,078E-12	8,2412E-31	7,251E-31	20,6639592	*3650*
200 wolves	7,7988E-30	-5,05E-13	1,1288E-30	9,9319E-31	20,6782264	*3650*
220 wolves	0,49341051	0,36959217	0,17574995	0,19384222	1277,121	*1001*
240 wolves	0,00294408	0,00078377	0,00041711	0,00036666	27,3819973	*3650*
260 wolves	5,0169E-10	1,3302E-10	7,1884E-11	6,3224E-11	23,3679787	*3650*
280 wolves	1,9217E-13	-1,418E-12	2,7637E-14	2,431E-14	22,3028046	*3650*
300 wolves	8,4618E-17	-2,045E-12	1,2193E-17	1,0726E-17	21,7910679	*3650*

If the assumption would be made that less than 0,001 carcasses would lead to extinction of the disease, extinction would occur earlier when the number of wolves increases from 1 to 140 (see Table 10). However, from 180 wolves the time to extinction increases again. This might be due to later onset of the outbreak, as shown in Figure 8. As mentioned before, the number of carcasses for 220 and 240 wolves never falls below 0,001.

Table 10: Time at which the number of carcasses fall below 0,001

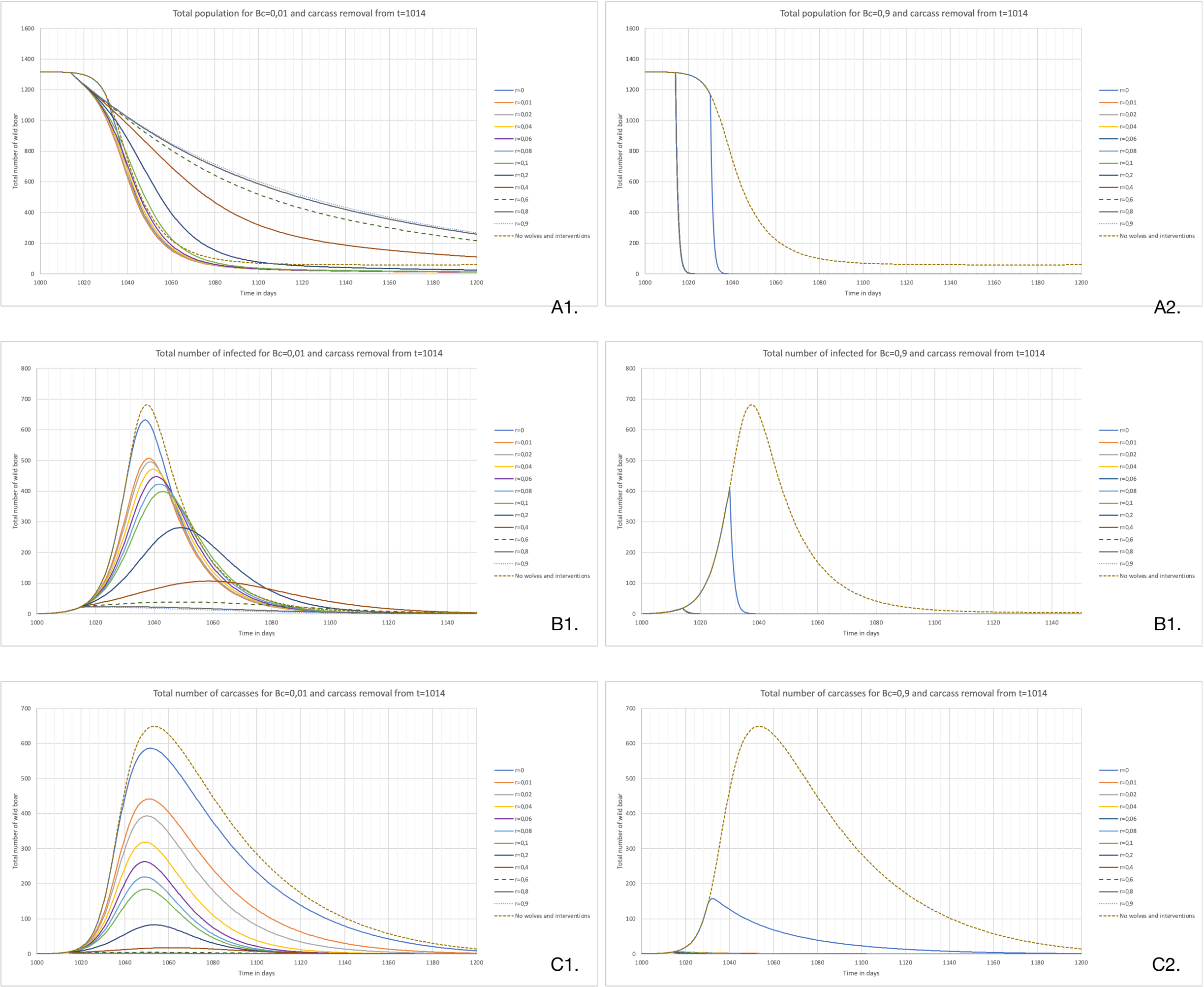
	Number of carcasses	Infected population	Number of infected adults	Number of infected piglets	Total population	*Time in days*
1 wolf	0,00099699	0,00127857	0,00054605	0,00073252	90,1917936	*2401*
10 wolves	0,00099045	0,00127932	0,00053438	0,00074494	75,2647895	*1660*
20 wolves	0,00099617	0,00030883	0,000108	0,00020083	35,6832757	*1411,5*
40 wolves	0,00099041	0,00042388	0,00013901	0,00028487	25,516923	*1345*
60 wolves	0,00099783	0,00062693	0,00017897	0,00044796	24,6485194	*1320,5*
80 wolves	0,00099151	0,00070123	0,00019003	0,0005112	24,4111215	*1311,5*
100 wolves	0,00099259	0,00072936	0,00019457	0,00053478	24,4025086	*1308*
120 wolves	0,0009813	0,00073133	0,00019394	0,00053739	24,4215292	*1306,5*
140 wolves	0,00099614	0,00074804	0,00019735	0,00055069	24,4501591	*1305,5*
160 wolves	0,00099328	0,00074066	0,0001954	0,00054526	24,4884532	*1306*
180 wolves	0,00098805	0,0007157	0,00019017	0,00052553	24,5462693	*1308,5*
200 wolves	0,00098531	0,00062677	0,00017244	0,00045433	24,685716	*1318*
220 wolves	-	-	-	-	-	-
240 wolves	-	-	-	-	-	-
260 wolves	0,00099756	0,00076848	0,00042748	0,000341	26,6594025	*3087,5*
280 wolves	0,00099404	0,00096707	0,0005507	0,00041637	26,8498259	*2748,5*
300 wolves	0,00099356	0,00060849	0,0003489	0,00025959	27,8757886	*2428*

Scenario 5: The combined effect of culling and carcass removal

The combined intervention of culling and carcass removal was modeled for a total of 972 outbreak scenarios. The culling and carcass removal rate were varied from 0,01 to 0,9, similar to the earlier mentioned scenarios, in 18 steps. The two intervention methods were initiated together at 3 different time points (1014, 1030 and 1180). The carcass transmission rate was set at 0,0008.

If carcass removal and culling is initiated at 14 days after introduction of ASF, a lower culling rate and a higher carcass removal rate will decrease the peak number of infected and carcasses compared to a situation with only culling or no interventions (see Figure 10). However, the duration of the outbreak increases when the carcass removal rate is higher. The number of wild boars decreases less dramatically when the carcass removal rate increases, but in all scenarios the population eventually becomes extinct (for r=0,01 and b_C=0,01 after 1504 days and for r=0,9 and b_C=0,01 after 1899 days). ASF will also be extinguished in all scenarios. This will happen faster if the carcass removal rate is higher. Under the assumption that the disease is extinct when the number of carcasses falls below 0,001, a culling rate of 0,01 and a carcass removal rate of 0,01 causes extinction after 1286 days. The same culling rate and a carcass removal rate of 0,9 will cause eradication of ASF after 1208 days. If culling is increased to 90%, carcass removal will lead to a faster extinction of the disease compared to a situation without carcass removal. ASF will become extinct after 1213 and 1025 days for a carcass removal rate of 0,01 and 0,9 respectively. For all carcass removal rates the population will become extinct at day 1022. Moreover, the maximum number of infected boars never exceeds 18.

Overall, a lower carcass removal rate and a higher culling rate will cause the population to go extinct earlier. However, a higher carcass removal rate will lead to earlier extinction of the disease.



A1.
A2.
B1.
B1.
C1.
C2.

Figure 10: The course of the initial ASF outbreak for different carcass removal rates (*r*) and culling rates (b_c). Carcass removal and culling was started at day 1014 and the carcass transmission rate was 0,0008.; **A**.: The total population wild boar for a culling rate of 0,01 (*A1.*) and 0,9 (*A2.*).; **B**.: The number of infected for a culling rate of 0,01 (*B1.*) and 0,9 (*B2.*).; **C**. The number of carcasses for a culling rate of 0,01 (*C1.*) and 0,9 (*C2.*).

Similar to the previous scenario, if culling and carcass removal are started at day 1030, the peak number of infected and carcasses is reduced if the culling rate and carcass removal rate is higher (see Figure 11). Moreover, a lower carcass removal rate and a higher culling rate will also cause the population to go extinct earlier in this scenario and a higher carcass removal rate will also lead to earlier extinction of the disease. However, the peak number of infected animals is higher compared to when both interventions are implemented at day 1014.

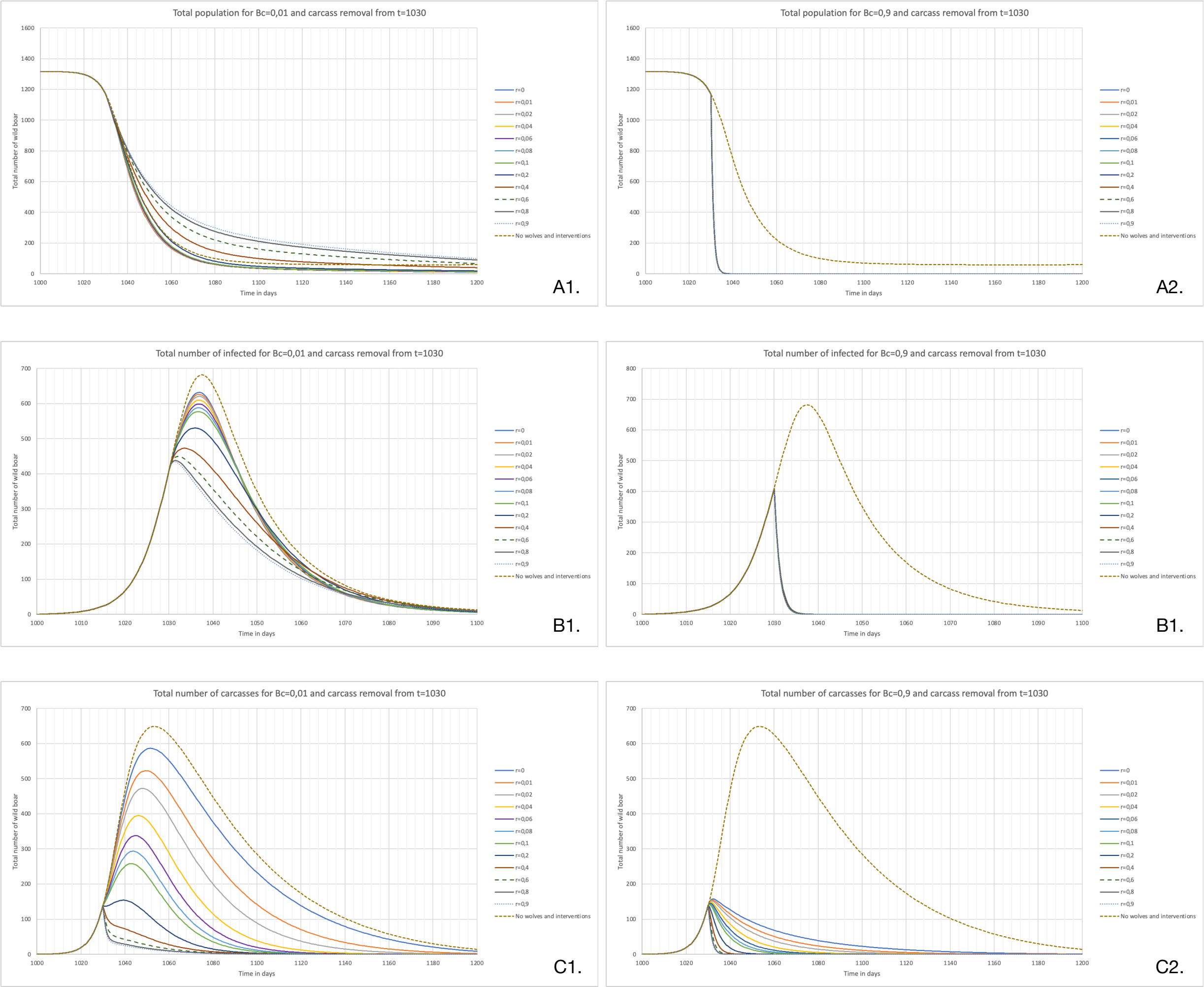


Figure 11: The course of the initial ASF outbreak for different carcass removal rates (*r*) and culling rates (b_C). Carcass removal and culling was started at day 1030 and the carcass transmission rate was 0,0008.; **A**.: The total population wild boar for a culling rate of 0,01 (*A1.*) and 0,9 (*A2.*).; **B**.: The number of infected for a culling rate of 0,01 (*B1.*) and 0,9 (*B2.*).; **C**. The number of carcasses for a culling rate of 0,01 (*C1.*) and 0,9 (*C2.*).

As can be observed in Figure 12, starting carcass removal and culling at day 1180 has no effect on the initial outbreak. However, the combined intervention of carcass removal and culling causes the population and disease to become extinct in all the outbreak scenarios. Similar to when both interventions are initiated at day 1014 and day 1030, a higher carcass removal rate causes the extinction of ASF to occur faster and the extinction of the population to occur later. If the culling rate and the carcass removal rate is 0,01 for example, extinction of ASF and the population of wild boars occur at day 1338 and 1698 respectively. A carcass removal rate of 0,9 and culling rate of 0,01 causes extinction to occur at day 1247 and 1703 respectively. However, if the culling rate is 0,9, extinction of the population will happen at day 1185 independent of the carcass removal rate.

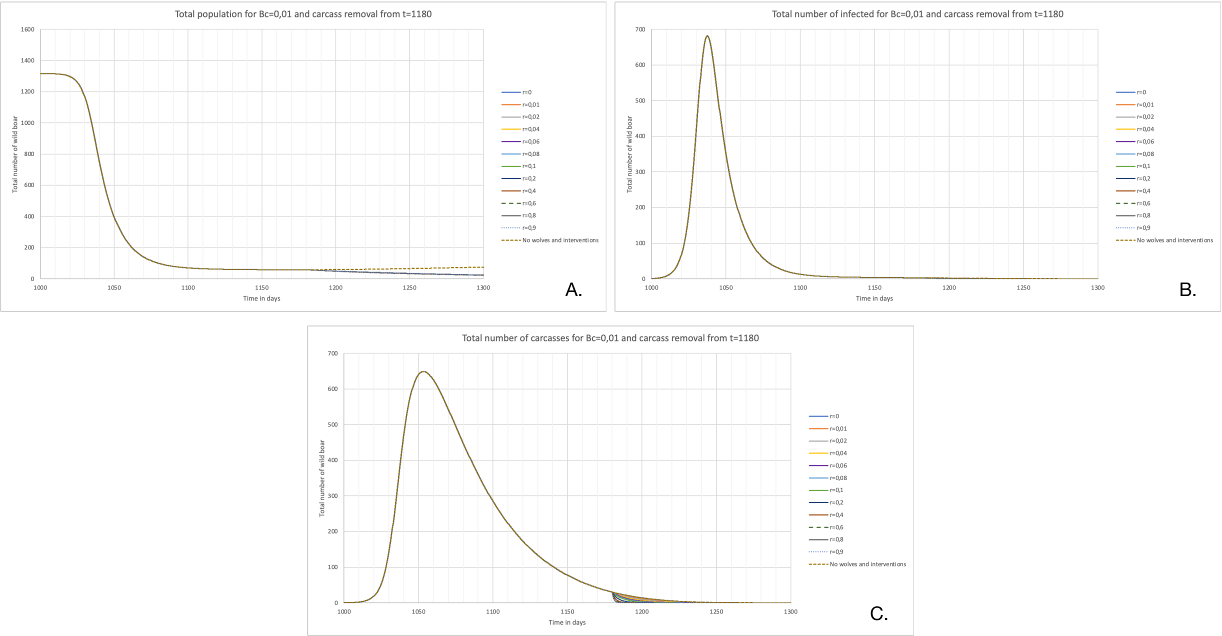


Figure 12: The course of the initial ASF outbreak for different carcass removal rates (*r*) and a culling rate (b_C) of 0,01. Carcass removal and culling was started at day 1180 and the carcass transmission rate was 0,0008.; **A**.: The total population wild boar for a culling rate of 0,01.; **B**.: The number of infected for a culling rate of 0,01.; **C**. The number of carcasses for a culling rate of 0,01.

Scenario 6: The combined effect of culling and the wolf

In this scenario the effect of the wolf was, similar to other scenarios, modeled for 1 to 300 wolves (16 steps in total) and the culling rate was varied from 0,01 to 0,9 in 18 steps and started at 3 different time points (day 1014, 1030 and 1180). This led to 864 different outbreak dynamics.

If culling is started at day 1014, the peak number of infected and carcasses is lower if the culling rate and the number of wolves is higher (see Figure 13). However, the duration of the outbreak is longer and the total number of wild boars decreases less steeply if there are more wolves present.

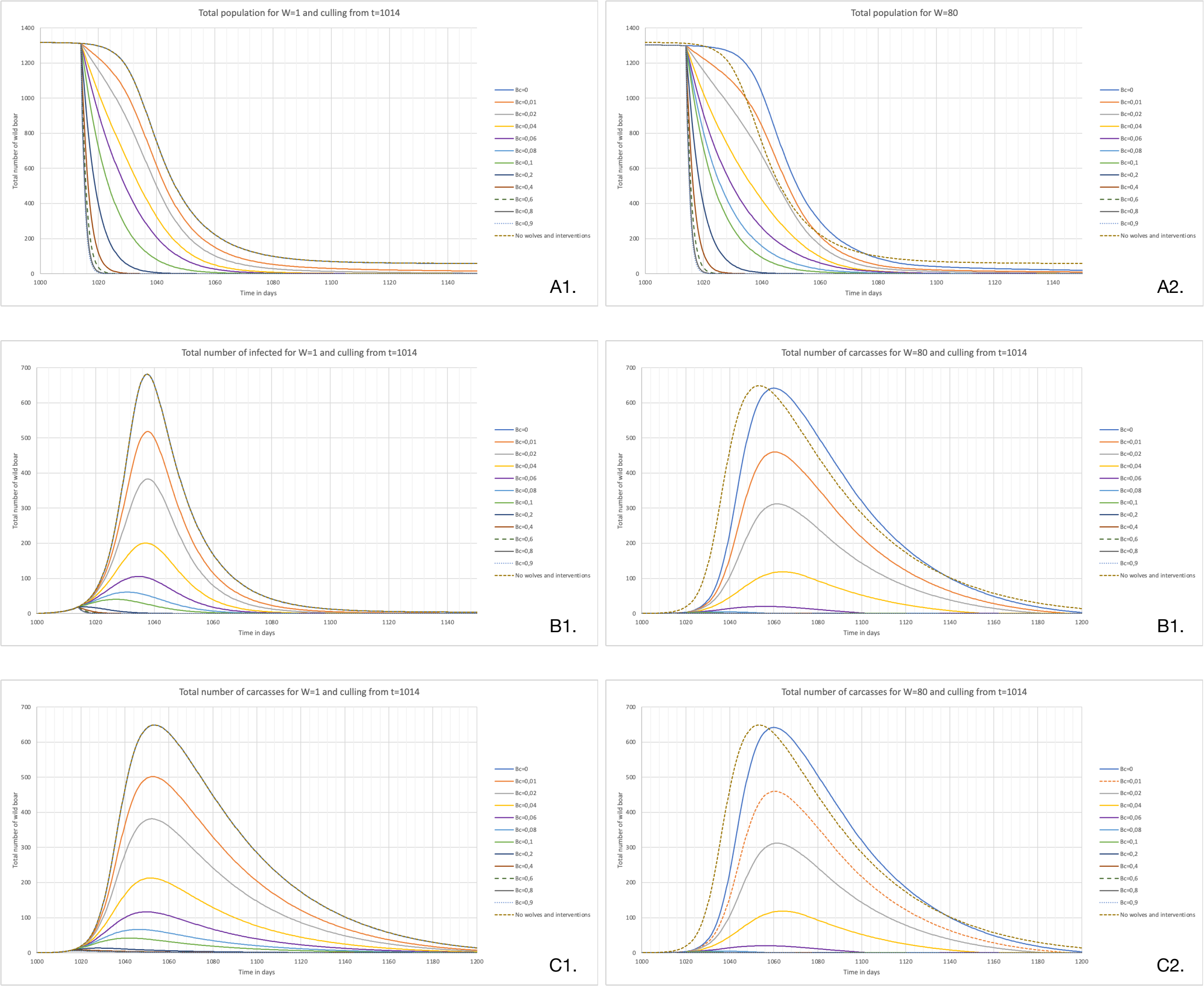


Figure 13: The course of the initial ASF outbreak for different numbers of wolves (*W*) and culling rates (b_c). Culling was started at day 1014 and the carcass transmission rate was 0,0008; **A.**: The total population wild boar for 1 wolf (*A1.*) and 80 wolves (*A2.*).; **B.**: The number of infected for 1 wolf (*B1.*) and 80 wolves (*B2.*).; **C.** The number of carcasses for 1 wolf (*C1.*) and 80 wolves (*C2.*).

Similar to the previous scenario, if culling is initiated at day 1030, the peak number of infected and carcasses is reduced if the culling rate and number of wolves are larger (see Figure 14). Moreover, if more wolves are present the outbreak takes place at a later time point, which decreases the peak number of infected even more.

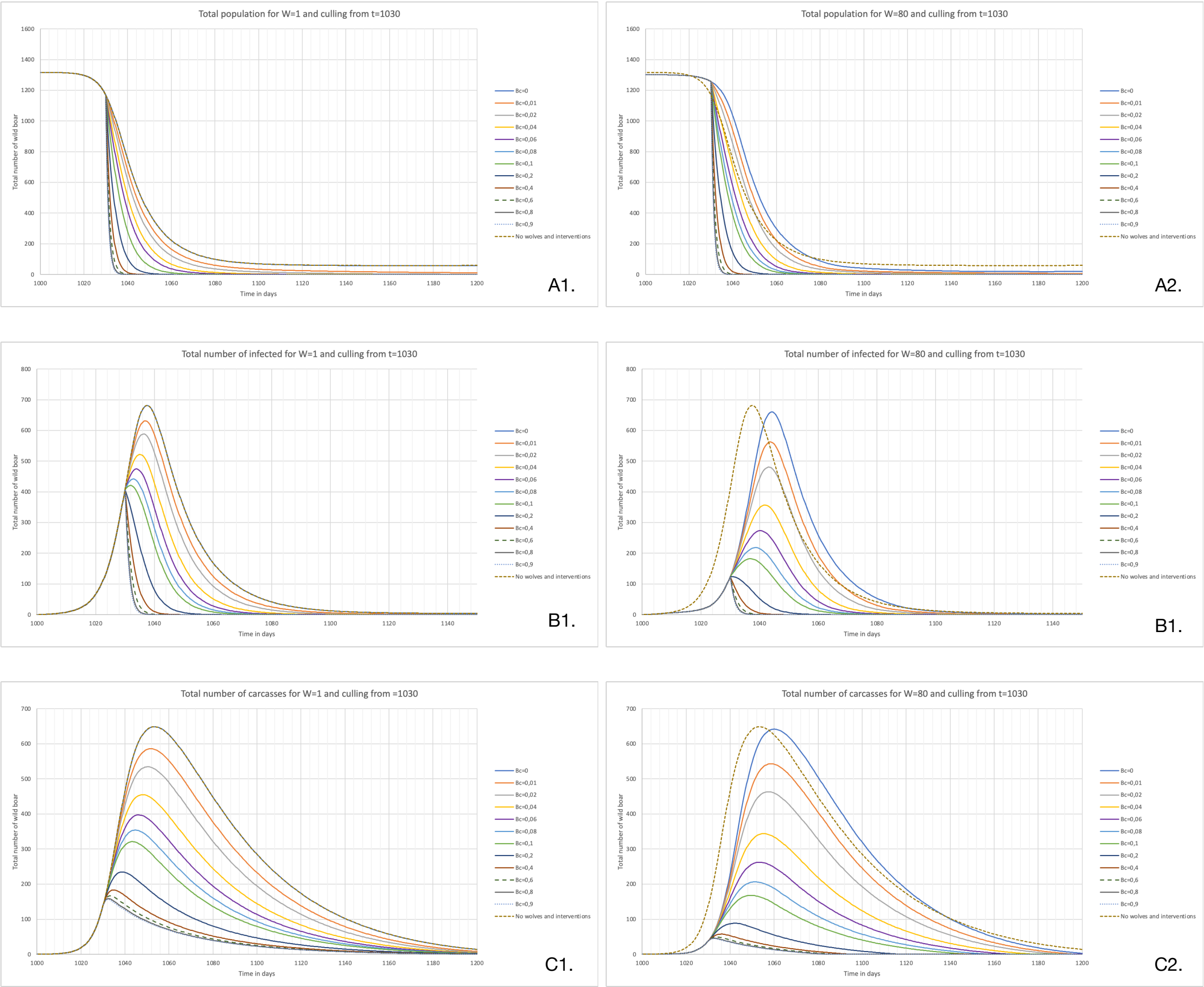


Figure 14: The course of the initial ASF outbreak for different numbers of wolves (*W*) and culling rates (*bc*). Culling was started at day 1030 and the carcass transmission rate was 0,0008.; **A**.: The total population wild boar for 1 wolf (*A1.*) and 80 wolves (*A2.*).; **B**.: The number of infected for 1 wolf (*B1.*) and 80 wolves (*B2.*).; **C**. The number of carcasses for 1 wolf (*C1.*) and 80 wolves (*C2.*).

If culling is started at day 1180 after introduction of ASF, it only influences the survival of ASF in the wild boar population (see Figure 15). It has no effect on the initial outbreak. In all disease scenarios the wild boar population goes extinct. The culling rate and number of wolves only influence how fast the population is extinguished (e.g., at day 1693 and 1554 for a culling rate of 0,01 and 1 and 80 wolves, respectively).

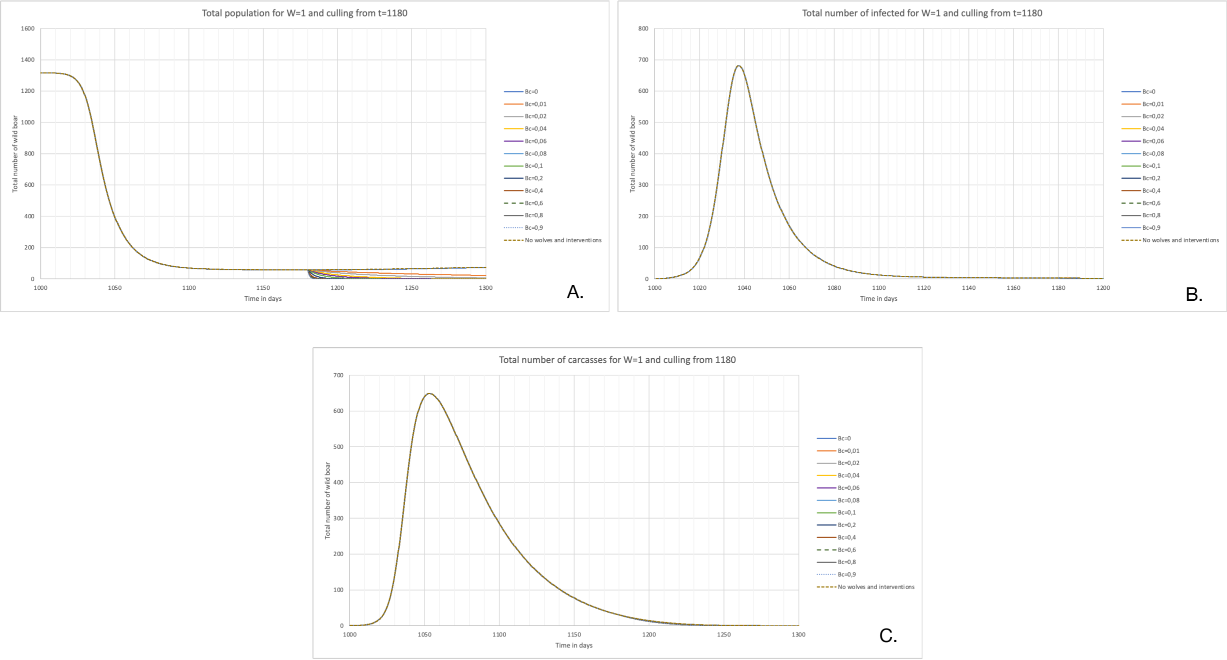


Figure 15: The course of the initial ASF outbreak for different culling rates (*b*c) and 1 wolf (*W*). Culling was started at day 1180 and the carcass transmission rate was 0,0008.; **A**.: The total population wild boar for 1 wolf.; **B**.: The number of infected for 1 wolf.; **C**. The number of carcasses for 1 wolf.

Scenario 7: The combined effect of carcass removal and the wolf

To model the combined effect of carcass removal and the wolf, a carcass transmission rate of 0,0008 was assumed and for each defined number of wolves (ranging from 1 to 300 in 7 steps) a carcass removal rate from 0,01 to 0,9 was started at 14, 30 and 180 days after introduction of ASF. This led to the modeling of 336 different outbreak scenarios.

As can be observed in Figure 12, if carcass removal would start at day 1014, the population would decrease less drastically and the peak number of carcasses and infected will be lower if the carcass removal rate and the number of wolves is higher. However, the outbreak will take off later if the number of wolves is higher. If there are 80 wolves present and if there is a carcass removal rate of 0,7 or more the total number of wild boars stays similar to that before the introduction of ASF (it will never fall below 1271 animals) and no more than 14 animals are infected at any time point. However, ASF will never disappear from the environment, as the number of carcasses never falls below 0,49 and stays fluctuating around 0,99 for most of the time. This might also be partly due to the aforementioned code *ifelse(D>= 1, W*bwp, 0)*, which prohibits wolves from eating carcasses if there is more than 1 carcass left.

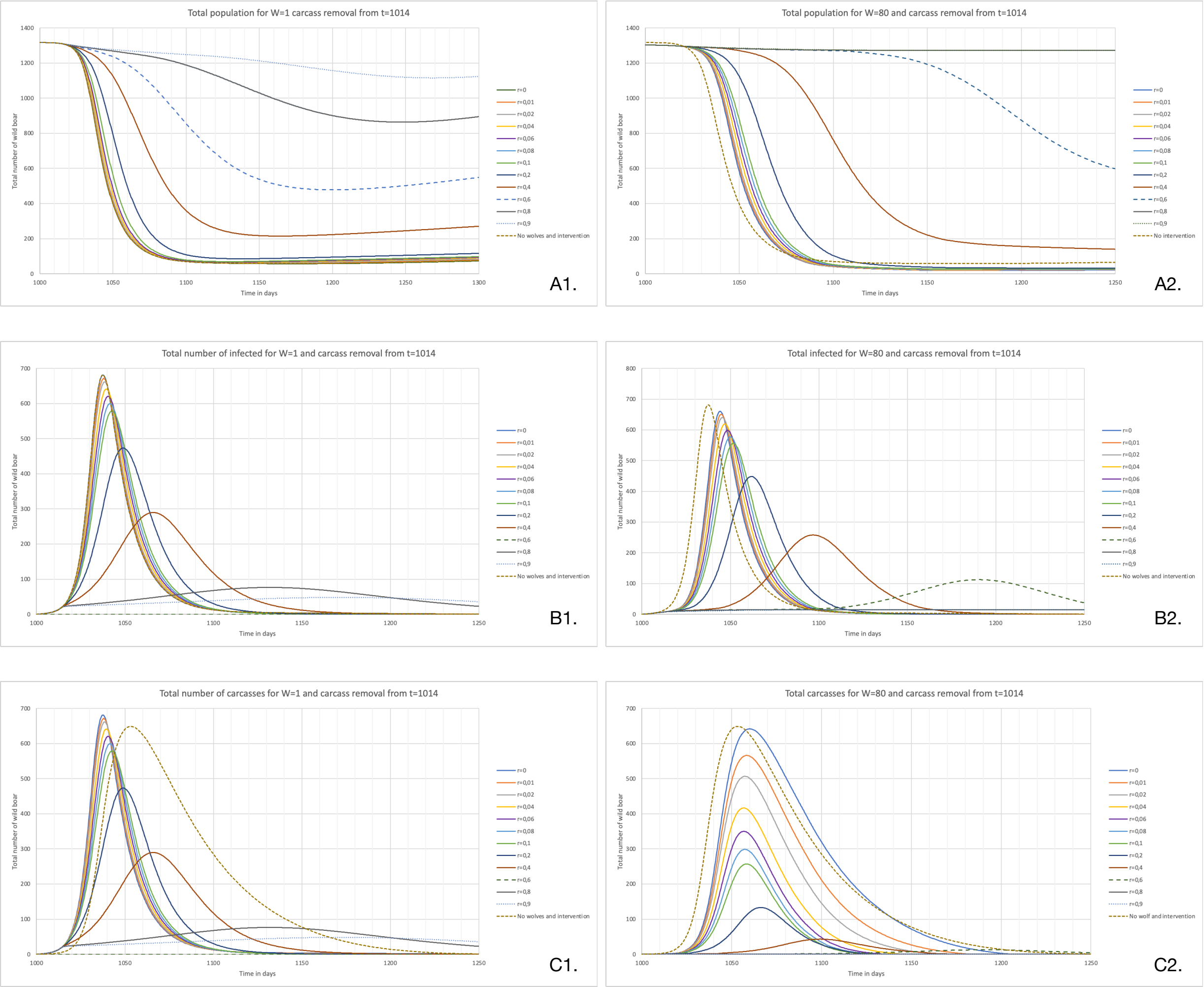


Figure 16: The course of the initial ASF outbreak for different numbers of wolves (*W*) and carcass removal rates (*r*). Carcass removal was started at day 1014 and the carcass transmission rate was 0,0008.; **A**.: The total population wild boar for 1 wolf (*A1.*) and 80 wolves (*A2.*).; **B**.: The number of infected for 1 wolf (*B1.*) and 80 wolves (*B2.*).; **C**. The number of carcasses for 1 wolf (*C1.*) and 80 wolves (*C2.*).

If the removal of carcasses would start 30 days after introduction of ASF, a large outbreak cannot be prevented, as would be the case when carcass removal starts at a high rate at day 14 with a larger number of wolves. However, a greater number of wolves can reduce the peak number infected animals (see Figure 17). Moreover, the population of wild boar decreases less dramatically when there are more wolves, and the carcass removal rate is higher. Interestingly, a larger number of wolves also causes a larger peak number of carcasses in the environment compared to a lower number of wolves for the same carcass removal rates. This might be due to more wild boars staying alive and thus more animals remaining that can be infected. However, the number of carcasses never gets high enough to infect sufficient animals to cause a further decline in the population, due to the removal of carcasses and the wolves eating carcasses. Thus, causing a longer presence of a larger number of carcasses in the environment.

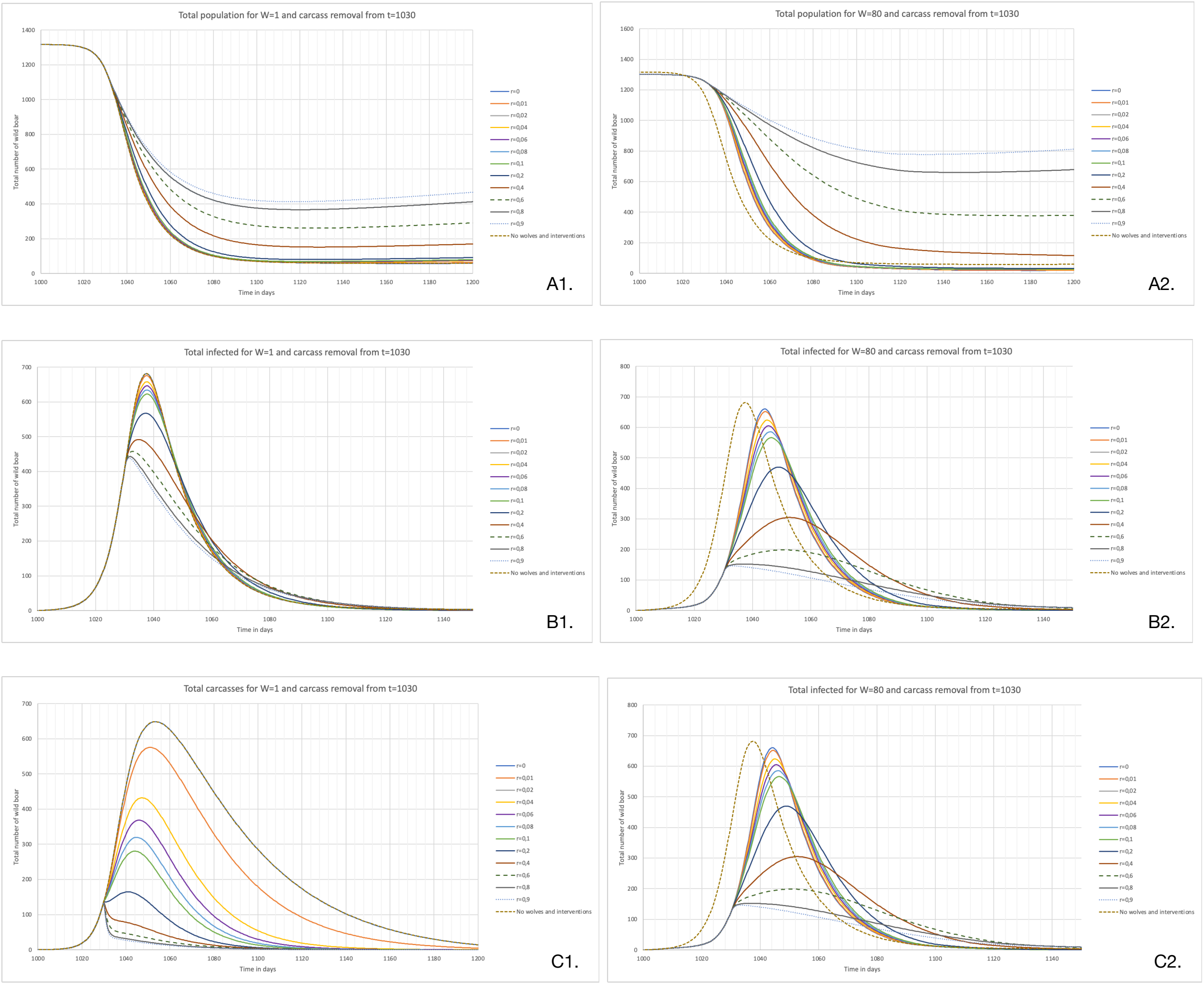


Figure 17: The course of the initial ASF outbreak for different numbers of wolves (*W*) and carcass removal rates (*r*). Carcass removal was started at day 1030 and the carcass transmission rate was 0,0008.; **A**.: The total population wild boar for 1 wolf (*A1.*) and 80 wolves (*A2.*).; **B**.: The number of infected for 1 wolf (*B1.*) and 80 wolves (*B2.*).; **C**. The number of carcasses for 1 wolf (*C1.*) and 80 wolves (*C2.*).

Similar to the situation when carcass removal would be initiated 180 days after introduction of ASF if no wolves are present, the carcass removal at that time point has also little effect on the disease dynamics in the case wolves are present (see Figure 18). However, different from a situation without wolves, the population of wild boar does not recover anymore if a large number of wolves are present.

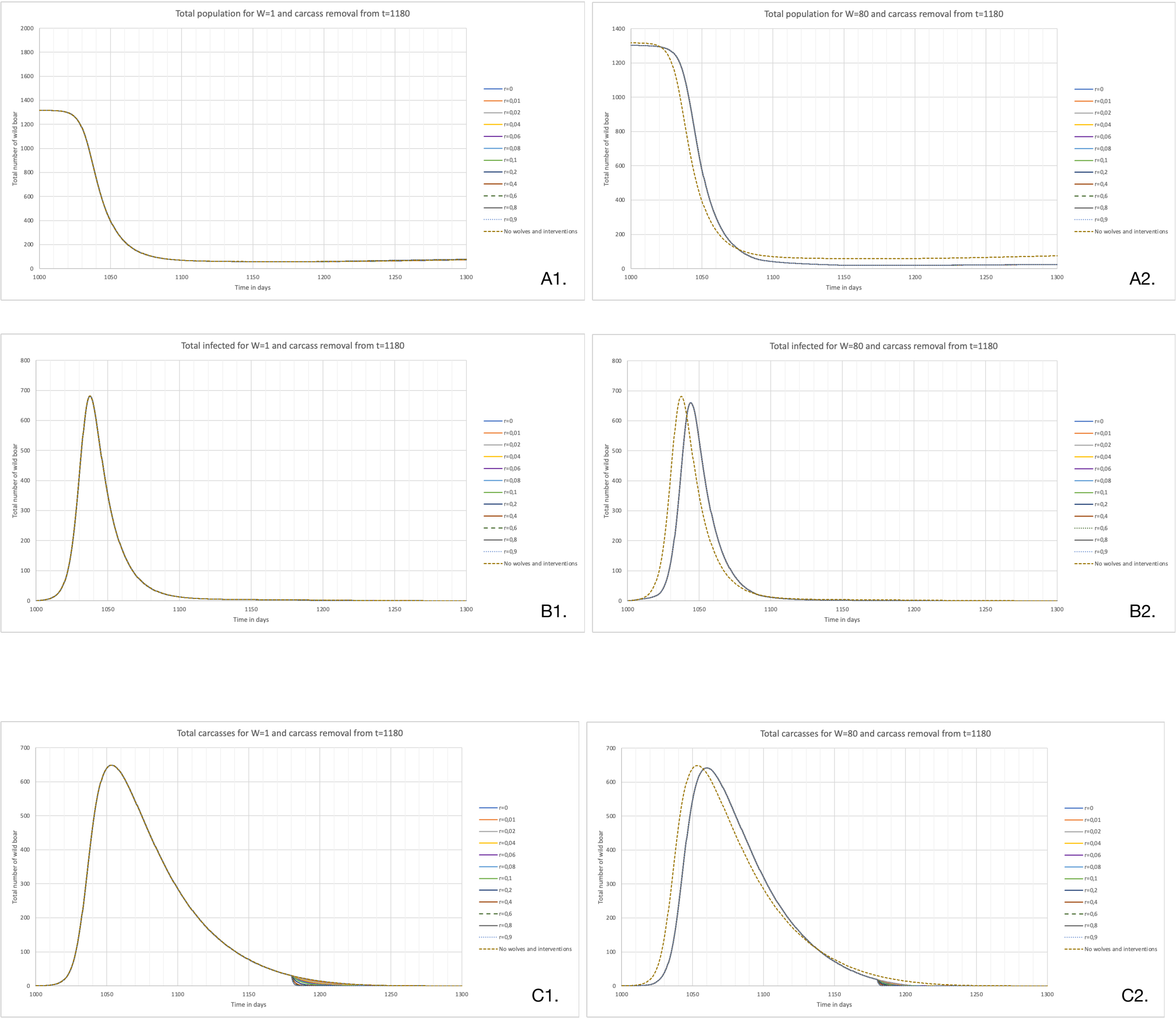


Figure 18: The course of the initial ASF outbreak for different numbers of wolves (*W*) and carcass removal rates (*r*). Carcass removal was started at day 1180 and the carcass transmission rate was 0,0008.; **A**.: The total population wild boar for 1 wolf (*A1.*) and 80 wolves (*A2.*).; **B**.: The number of infected for 1 wolf (*B1.*) and 80 wolves (*B2.*).; **C**. The number of carcasses for 1 wolf (*C1.*) and 80 wolves (*C2.*).

Scenario 8: The combined effect of both interventions and the wolf

A total of 1344 outbreak scenarios were modeled to asses the combined effect of the wolf, culling and carcass removal. The number of wolves ranged from 1 to 300 in 7 steps and the culling rate and carcass removal rate were both varied from 0,01 to 0,8 in 8 steps. The intervention methods (culling and carcass removal) were implemented together at 14, 30 and 180 days after introduction of ASF.

In the time frame of this thesis, insufficient results were produced to analyze the combined effect of culling, carcass removal and the wolf.

Discussion

This thesis shows that a mathematical model can be useful to explore scenarios of African Swine fever control in wild boar populations under the influence of predation by wolves. It was shown that a model can be developed that takes the key processes into account for such an interaction between wild boar, ASF and wolves and how such a model can be used to assess 'what if'-scenarios of various kinds. In the absence of wolves and ASF, and when parameterized for the nature reserve 'De Hoge Veluwe' in the Netherlands, the model calculations show that the equilibrium number of wild boars is close to the observed level, thus providing a minimum validation. The thesis documents the context for the model and its development and shows how it can be used to analyze scenarios for a broad range of parameter values for key parameters. This shows both the usefulness and flexibility, but the initial exploration also highlights where the model and the way it is analyzed can be improved.

The results flowing out of this model suggest that the wolf has the potential to influence the disease dynamics during an ASF outbreak in the Netherlands. Wolves were found to decrease the peak number of infected wild boar and to shift the outbreak to a later time point. Moreover, in this model the wolf formed a valuable asset to the implementation of intervention methods. A higher number of wolves reduced the intensity of the intervention methods needed to either reduce the size of an ASF outbreak or to eradicate an ASF outbreak. Moreover, in the case that carcass removal would be the only intervention and if it would be implemented early (14 or 30 days post introduction of ASF), the wolf can help mitigate a crash in the number of wild boar due to ASF. Therefore, the wolf could help to maintain a healthier population size of wild boar. However, if carcass removal would be implemented later (180 days post introduction of ASF), the wolf can prevent the population of wild boar from recovering. Another effect of the wolf is that the outbreak occurs at a later time point and that the outbreak has a longer duration. The later occurrence of the outbreak might be due to the wolf eating some of the first occurring carcasses and therefore delaying onset of the outbreak. This has both benefits and disadvantages. On one side it would allow more time to notice an ASF introduction and interventions that are started later can still reduce the impact of the initial outbreak. However, a longer duration of the outbreak, would also increase the risk of the disease spreading to other locations.

Nonetheless, models are, as a rule, simplified representations of reality. Also in this model, many factors are not taken into account, like breeding seasons, migration and fluctuations in seasonal food availability (and thus mortality). The wild boar population in this model also has only two age classes, while yearlings are often considered a separate age group from adults and piglets. Moreover, no spatial information is considered in this model. This is especially relevant regarding the group dynamics of wild boar, in which young males often migrate to other areas and groups of females live separated from adult males for most of the time (Morelle et al., 2015). Natural and artificial blockades (like highways and large bodies of water), suitability of land and food availability can also play a role in the dispersal and density of wild boar populations and therefore influence disease dynamics (Morelle et al., 2015). Many infected wild boar carcasses with ASF were for example found near bodies of water. It is thought that these wild boars might have sought a cool spot to reduce their fever (Sauter-Louis et al., 2021). As these water bodies also attract a lot of other wild boar that want to drink water, this might for example form a local hot spot for transmission. Another reason that spatial factors could play a role in transmission is though the creation of a landscape of fear through culling or hunting by the wolf (Kuijper et al., 2013; Thurfjell, Spong, & Ericsson, 2013). This might concentrate animals in areas that are deemed safer or cause dispersal to other areas, which in turn could affect transmission of ASF.

The wolf population is assumed to be constant in this model, but in reality a population of wolves is of course dynamic. Just like with wild boar, there is also a spatial dynamic in the behavior of the wolf. A pack has a certain territory in which it hunts, and younger wolves often migrate to find a new territory to settle (Mech & Peterson, 2003/2006b). The size of a territory can, for example, influence the number of wolves that are hunting in a certain area. Moreover, the amount of consumption of several types of prey might fluctuates over the year due to availability. During the breeding season of a prey species, the wolf might for example prefer to hunt specific prey species over others as the species is more abundant and more weak young animals are available (Mech & Peterson, 2003/2006a). Wagner et al. (2011) found that wolves in Germany eat proportionally more wild boars in winter and spring and less in summer and autumn, when there are more deer present. Moreover, the hard cut-off point used in this model for when wolves stop hunting wild boar, is probably more diffuse in reality. It is also not known at what point wolves start to prefer other prey. Furthermore, it is not known how many carcasses a wolf consumes, especially if they are not caught by a wolf itself. Wolves have been filmed scavenging carcasses in the Netherlands and frequent carrion consumption by wolves has been found common for wolves in Denali National Park (United States) (Dooddoetleven, 2020; Klauder et al., 2021). However, more research has to be done to assess the amount of either scavenged or hunted carcasses that is consumed by wolves. In this model there is no distinction made between infected carcasses created by the wolf and infected carcasses created through disease mortality. Therefore, this could make the number of carcasses consumed by the wolf either higher or lower than in reality.

The use of a deterministic compartmental model has some important connotations (Diekmann et al., 2013). Firstly, a deterministic model assumes that population is so large that chance variation can be ignored, i.e., the model excludes all stochastic elements in the parameters. In reality one animal could stay infected for 7 days for example while others stay infected for two weeks. In this model all animals stay infected for on average 14 days. In small populations this can be different by chance. Another problem is that the probability for an individual to still be present in a compartment never truly reaches zero, as this probability decreases exponentially by the nature of the compartmental model. This could, for example, cause a new outbreak to occur, even if the probability that there would still be infected animals and infected carcasses has fallen to such a low point, that this would be very unlikely. Because deterministic models assume that the population size is very large, there can still be animals in these compartments also after an unrealistically long time. Effectively, in small populations, the infection would have died out long before and hence a new outbreak is not possible without reintroduction of the disease from outside. A third problem is that only proportions of a population move between compartments and not whole animals. Again, in large populations this is not an issue, but in small populations it becomes important that in reality one deals with whole animals and whole carcasses. This also forms a problem for the age classes, as only proportions of animals in the piglet compartments grow up during the year instead of all piglets moving to the adult compartments after exactly one year after they are born.

Regarding this model, more development and analysis is needed to improve its current form and use. A large range of sensitivity testing has to be done to test the effect of all parameters on the course of the outbreak. A more meticulous set of runs has to be done to exactly find the right carcass transmission rate. These runs have to be compared to field data in more detail to find the most suiting carcass transmission rate. Moreover, the harsh cut-off points regarding hunting and scavenging of the wolf might have to be reconsidered as should the way in which these are modeled. The cut-off point regarding carcasses might have caused the model to behave unexpectedly when it reached 220-300 wolves. The cut-off points for hunting by the wolf were in this model regulated per compartment and regulated for the total population. Therefore, if there would have been fewer than 10 susceptible in a compartment but more than 10 recovered in the other, the wolf would only hunt recovered animals. This would of course be unrealistic. Another problem in relation to hunting by the wolf is that its dietary consumption is divided by three (for adults, piglets and carcasses), but no division is made for the three compartments of piglets and adults (susceptible, infected and recovered). This could have led to overconsumption of wild boar by these fictional wolves. The same problem exists with regard to culling. The culling rate has also not been divided by the number of compartments, making the culling rate cumulatively higher for the whole population. A culling rate made more proportional to the number of compartments, might have caused less dramatic effects with regard to extinction of the population.

Moreover, due to time constraints, a lot of numerical analyses have not been done to further examine the results. More should be done to determine mistakes made during programming or processing of the data and to understand how the model behaves under different parameters and variables.

Overall, this is one of the first models that looks at the relationship between wolves, wild boar and African Swine Fever. This model does seem to suggest that the wolf influences disease dynamics and interventions. As with any initial exploration, this novel model has many shortcomings but seems sufficiently promising to be further developed, together with more field and clinical research on ASF, to study the questions and the results in more detail.

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Annex 1: Outbreak without wolves or interventions

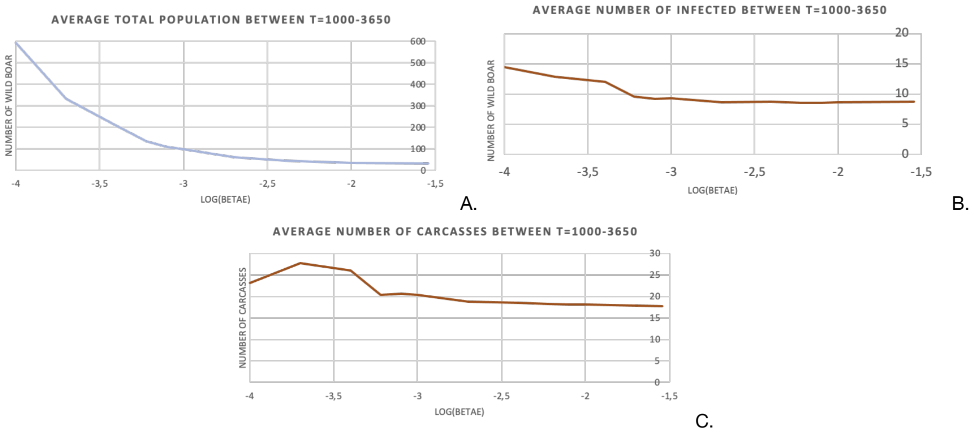


Figure I: The effect of the carcass transmission rate (*BetaE*) on the averages of the total population (**A**.), the number of infected (**B**.) and the number of carcasses (**C**.)

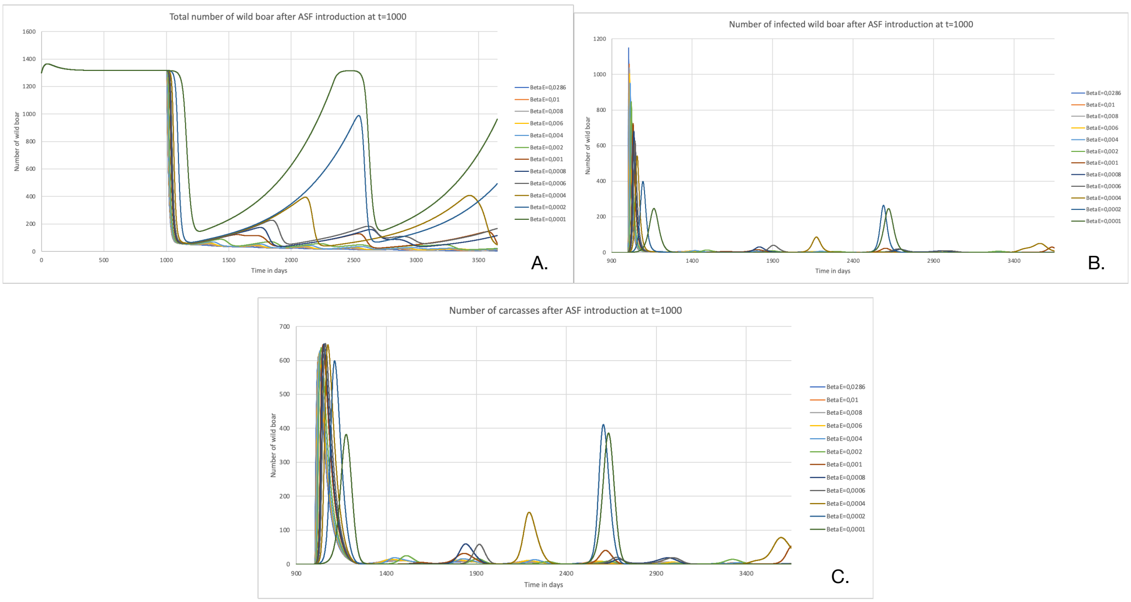


Figure II: The course of the disease after ASF is introduced at a 1000 days for different carcass transmission rates (*BetaE*). **A**.: The total population wild boar; **B**.: The total number of infected; **C**. The total number of carcasses.

Annex 2: Outbreak with carcass removal

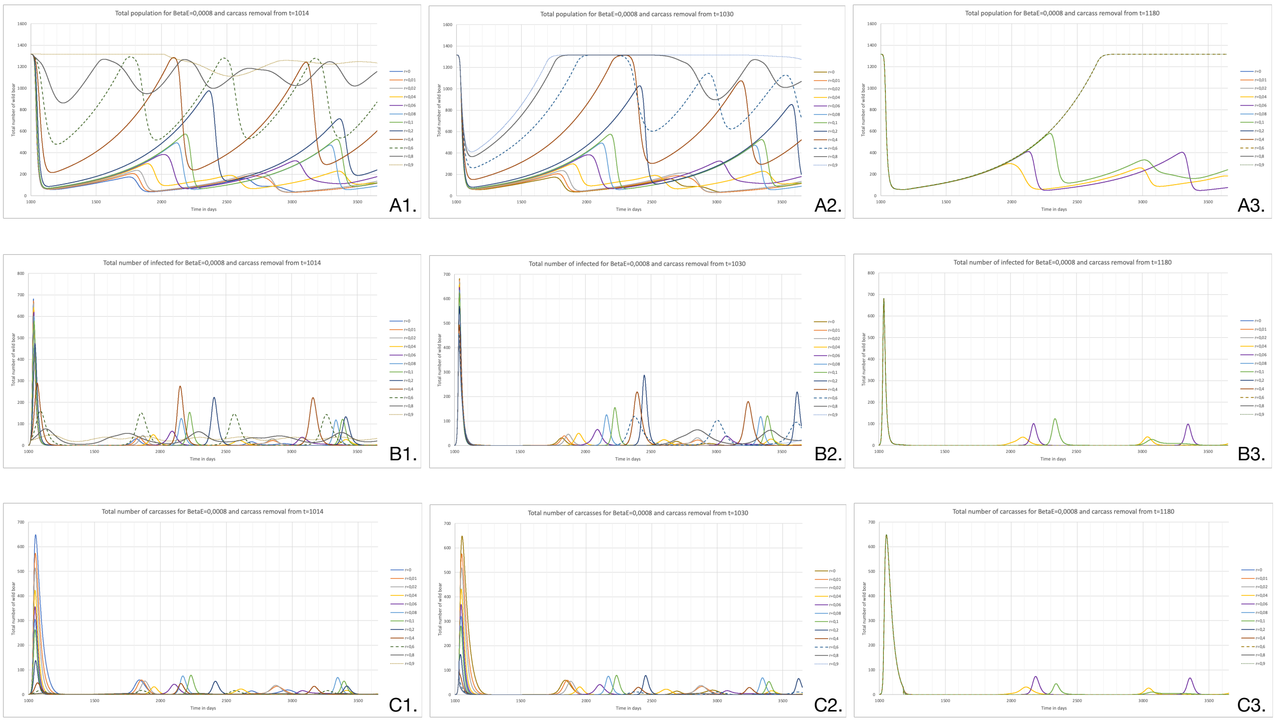


Fig. **III**: The course of the disease after ASF is introduced at a 1000 days for different carcass removal rates (*r*) and a carcass transmission rate (*BetaE*) of 0,0008. **A**.: The total population wild boar for carcass removal started at day 1014 (*A1.*), day 1030 (*A2.*) and day 1180 (*A3.*); **B**.: The number of infected for carcass removal started at day 1014 (*B1.*), day 1030 (*B2.*) and day 1180 (*B3.*); **C**. The number of carcasses for carcass removal started at day 1014 (*C1.*), day 1030 (*C2.*) and day 1180 (*C3.*)

Carcass removal at t=1014

Table I: The smallest number of wild boar for different carcass removal rates starting at t=1014 (BetaE=0,0008)

	Total population	Susceptible population	Number of suscepible adults	Number of susceptible piglets	Infected population	Number of infected adults	Number of infected piglets	Recovered population	Number of recovered adults	Number of recovered piglets	Number of carcasses	*Time in days*
No carcass removal	35,297179	21,706535	7,2149361	14,491598	1,3926054	0,5479132	0,8446922	12,198039	10,711139	1,4869001	3,009889	*3054,5*
r= 0,01	31,2255913	14,9272974	4,10499993	10,8222975	1,38481333	0,47598356	0,90882977	14,9134806	12,5376263	2,37585435	5,47691313	*2991,5*
r= 0,02	35,3026394	17,3240462	5,00796222	12,316084	1,5138716	0,55159755	0,96227404	16,4647216	13,5746605	2,89006115	4,79386325	*2979*
r= 0,03	60,1754491	31,5634793	9,97804062	21,5854387	2,64952232	1,13415158	1,51537074	25,9624475	21,793464	4,16898345	2,21519377	*1991*
r= 0,04	65,4750731	9,78053914	0,4766852	9,30385394	2,86993032	0,83127688	2,03865344	52,8246037	34,1951929	18,6294108	11,971591	*1130,5*
r= 0,05	58,3108292	37,6200829	13,5156266	24,1044563	2,14059167	0,91271376	1,22787791	18,5501546	15,3976263	3,15252829	2,65923599	*3011*
r= 0,06	65,8851427	35,3262238	11,2973324	24,0288914	2,66194638	1,07561404	1,58633234	27,8969725	22,5515363	5,34543624	3,54698556	*2200,5*
r= 0,07	48,4195548	21,8429933	6,46556683	15,3774264	1,93638826	0,85051351	1,08587475	24,6401732	18,3447344	6,2954388	2,451463	*3366,5*
r= 0,08	56,9710073	28,5676392	9,29114037	19,2764988	2,17174529	1,02465355	1,14709174	26,2316229	19,2687966	6,9628263	1,49529579	*3427,5*
r= 0,09	62,0727841	26,5163529	7,47019085	19,0461621	2,6169703	1,16052967	1,45644063	32,9394608	24,8729415	8,06651931	2,38858786	*2282,5*
r= 0,1	67,3557841	30,4024184	9,06320049	21,3392179	2,7728713	1,27725435	1,49561695	34,1804944	25,5101874	8,67030698	1,89430732	*2312*
r= 0,2	86,7117301	30,5285676	7,53441922	22,9941484	3,02060049	1,52559787	1,49500262	53,162562	34,2770515	18,8855105	1,27531375	*1136,5*
r= 0,3	133,611405	77,7137862	28,7844407	48,9293455	4,14198473	2,0989966	2,04298812	51,7556336	33,7734379	17,9821957	1,05525295	*1149,5*
r= 0,4	216,031547	160,155998	66,7056827	93,4503152	6,38916334	3,21299325	3,17617009	49,4863858	32,5882924	16,8980934	1,15907814	*1163,5*
r= 0,5	332,010522	276,146547	120,307017	155,83953	9,503583	4,74092466	4,76265834	46,3603922	30,8211592	15,539233	1,33311141	*1180*
r= 0,6	478,80462	422,598638	188,153714	234,444924	13,6119678	6,74752507	6,86444277	42,5940138	28,5683125	14,0257013	1,54760842	*1199*
r= 0,7	655,039213	598,52828	269,722205	328,806075	18,2072807	8,98209723	9,22518344	38,3036525	25,9405754	12,3630771	1,7215372	*1222*
r= 0,8	862,693889	805,259702	365,757304	439,502398	23,9021114	11,7519845	12,1501269	33,5320763	22,8295305	10,7025458	1,91203287	*1247*
r= 0,9	1111,35607	1053,46707	481,426253	572,040819	30,7107136	15,0532364	15,6574773	27,1782864	18,4263864	8,75190008	2,14222412	*1268*

Table II: The smallest number of carcasses for different carcass removal rates starting at t=1014 (BetaE=0,0008)

	Number of carcasses	Infected population	Number of infected adults	Number of infected piglets	total population	*Time in days*
No carcass removal	0,00312902	0,003435957	0,0015640	0,0018720	88,999211	*3516,5*
r= 0,01	4,1633E-05	4,6021E-05	2,078E-05	2,5241E-05	91,472431	*3525,5*
r= 0,02	2,0524E-05	2,6059E-05	1,1834E-05	1,4225E-05	105,424084	*3524*
r= 0,03	0,00108994	0,00098627	0,00030367	0,0006826	111,276424	*1396*
r= 0,04	0,00038324	0,0003803	0,00012322	0,00025709	118,630886	*1414*
r= 0,05	0,00010585	0,00023569	0,00010047	0,00013522	200,898185	*1667*
r= 0,06	1,9163E-05	4,3955E-05	1,8847E-05	2,5108E-05	205,505786	*1671,5*
r= 0,07	3,0179E-06	6,5487E-06	2,9619E-06	3,5868E-06	183,847602	*2781,5*
r= 0,08	5,0452E-07	1,0537E-06	4,7267E-07	5,8098E-07	180,548974	*2796*
r= 0,09	2,3974E-07	5,8948E-07	2,5614E-07	3,3334E-07	217,295311	*1686*
r= 0,1	7,2009E-08	1,8017E-07	7,8582E-08	1,0159E-07	221,576635	*1692*
r= 0,2	2,8678E-10	9,5374E-10	4,3197E-10	5,2188E-10	299,847744	*1757,5*
r= 0,3	6,0715E-09	2,9401E-08	1,3666E-08	1,5735E-08	425,170994	*1738*
r= 0,4	1,7767E-06	1,2292E-05	5,809E-06	6,4833E-06	588,33661	*1682*
r= 0,5	0,00038384	0,00336662	0,0015987	0,00176792	777,535142	*1630*
r= 0,6	0,01110544	0,09856555	0,04681981	0,05174574	778,506055	*1475*
r= 0,7	0,10009069	1,03251924	0,49415255	0,5383667	899,004385	*1424,5*
r= 0,8	0,46210095	5,46055293	2,63205906	2,82849388	1027,15091	*1393,5*
r= 0,9	0,49206108	0,37925	0,17539436	0,20385564	1316,79655	*1001*

Table III: The time at which the number of carcasses fall below 0,001 for different carcass removal rates starting at t=1014 (BetaE=0,0008)

	Number of carcasses	Infected population	Number of infected adults	Number of infected piglets	Total population	*Time in days*
r= 0,01	0,00099708	0,00150031	0,00063995	0,00086036	111,494766	*2397,5*
r= 0,02	0,00099878	0,00171685	0,00073287	0,00098398	117,164194	*2384*
r= 0,03	-	-	-	-	-	-
r= 0,04	0,00099953	0,00131686	0,00037889	0,00093796	98,7140256	*1325,5*
r= 0,05	0,00098635	0,00165299	0,00046746	0,00118553	96,0280968	*1303*
r= 0,06	0,00098015	0,00185342	0,00051733	0,00133609	94,6151445	*1289*
r= 0,07	0,00098724	0,00198106	0,0005506	0,00143046	93,6987495	*1279*
r= 0,08	0,00099921	0,00207685	0,00058067	0,00149618	93,0916756	*1271,5*
r= 0,09	0,00099667	0,00213724	0,00060724	0,00153	92,7818751	*1266*
r= 0,1	0,00098087	0,00217792	0,0006338	0,00154412	92,7462083	*1262*
r= 0,2	0,00097677	0,00345478	0,0013539	0,00210088	109,050752	*1255,5*
r= 0,3	0,00098301	0,00521256	0,00234944	0,00286312	169,658199	*1280*
r= 0,4	0,00099779	0,00625979	0,00293849	0,0033213	289,226317	*1327*
r= 0,5	0,0009977	0,00726545	0,00342557	0,00383988	521,581868	*1430*
r= 0,6	-	-	-	-	-	-
r= 0,7	-	-	-	-	-	-
r= 0,8	-	-	-	-	-	-
r= 0,9	-	-	-	-	-	-

Carcass removal at t=1030

Table IV: Lowest number of wild boar for different carcass removal rates starting at t=1030 (BetaE=0,0008)

	Total population	**Susceptible population**	**Number of suscepible adults**	**Number of susceptible piglets**	**Infected population**	**Number of infected adults**	**Number of infected piglets**	**Recovered population**	**Number of recovered adults**	**Number of recovered piglets**	**Number of carcasses**	***Time in days***
No carcass removal	35,297179	21,706535	7,2149361	14,491598	1,3926054	0,5479132	0,8446922	12,198039	10,711139	1,4869001	3,009889	*3054,5*
r= 0,01	31,1632165	14,8457337	10,7678525	4,07788122	1,39312747	0,47879858	0,91432889	14,9243553	12,5392547	2,38510057	5,54028234	*2991*
r= 0,02	35,1465382	17,1396403	12,1986491	4,94099113	1,52304607	0,55477348	0,9682726	16,4838519	13,5756511	2,9082008	4,86338838	*2978,5*
r= 0,03	59,9852778	31,4541776	21,528972	9,92520563	2,6080323	1,11566381	1,49236849	25,923068	21,7602371	4,1628309	2,18280602	*1991*
r= 0,04	65,3643856	9,76556014	9,28948785	0,47607229	2,85983314	0,82771539	2,03211775	52,7389923	34,1284359	18,6105564	11,9712141	*1129*
r= 0,05	58,9416304	38,3101706	24,4872317	13,8229389	2,16631598	0,92468435	1,24163163	18,4651438	15,3492025	3,11594127	2,66938263	*3011*
r= 0,06	66,1168061	35,606884	24,174249	11,432635	2,68309248	1,08577921	1,59731327	27,8268296	22,4922694	5,33456013	3,56177586	*2200*
r= 0,07	48,3907879	21,7813253	15,3247807	6,45654463	1,97048457	0,86654604	1,10393853	24,6389781	18,3290585	6,30991956	2,50095491	*3366*
r= 0,08	57,0709832	28,6994546	19,3521829	9,34727165	2,157617	1,01899827	1,13861873	26,2139116	19,2517624	6,96214917	1,46955659	*3428,5*
r= 0,09	61,8854905	26,3546428	18,9371022	7,41754054	2,62555198	1,16526485	1,46028713	32,9052957	24,8171478	8,08814798	2,40480936	*2282*
r= 0,1	67,134942	30,3146573	21,3046583	9,00999905	2,69791203	1,24254945	1,45536259	34,1223726	25,4527564	8,66961619	1,83769984	*2312,5*
r= 0,2	81,2806196	25,6194753	20,2472942	5,37218104	2,78283124	1,42446653	1,35836471	52,8783131	33,8972473	18,9810658	1,195634	*1125*
r= 0,3	109,396091	53,9371327	35,8360293	18,1011035	3,54684527	1,84478904	1,70205623	51,912113	33,3694765	18,5426365	0,93096899	*1127*
r= 0,4	152,791232	97,6589353	59,4368681	38,2220671	4,64047641	2,41362291	2,2268535	50,4918201	32,4721114	18,0197087	0,87641152	*1128*
r= 0,5	205,292146	150,483782	87,7407527	62,7430293	5,96984049	3,0997379	2,87010259	48,838524	31,3278303	17,5106937	0,88242738	*1127,5*
r= 0,6	260,986789	206,369871	117,554425	88,8154463	7,49270136	3,88693693	3,60576442	47,1242163	30,0596742	17,0645421	0,91165545	*1125,5*
r= 0,7	315,518981	260,986254	146,615188	114,371066	9,09099643	4,71645168	4,37454475	45,4417304	28,7699509	16,6717795	0,94127339	*1122,5*
r= 0,8	366,220947	311,991872	173,74751	138,244362	10,4130338	5,40657425	5,00645951	43,8160417	27,5454735	16,2705682	0,93914134	*1119,5*
r= 0,9	411,828589	358,009267	198,21217	159,797097	11,5058193	5,98221413	5,52360517	42,3135029	26,4196235	15,8938794	0,91972625	*1116,5*

Table V: Lowest number of carcasses for different carcass removal rates starting at t=1030 (BetaE=0,0008)

	Number of carcasses	**Infected population**	**Number of infected adults**	**Number of infected piglets**	**total population**	***Time in days***
No carcass removal	0,00312902	0,003435957	0,0015640	0,0018720	88,999211	*3516,5*
r= 0,01	4,0539E-05	4,4784E-05	2,022E-05	2,4564E-05	91,3471946	*3525,5*
r= 0,02	1,9204E-05	2,4348E-05	1,1055E-05	1,3293E-05	105,064821	*3524*
r= 0,03	0,00108099	0,00097964	0,00030201	0,00067763	111,23671	*1395,5*
r= 0,04	0,00037718	0,00037484	0,00012166	0,00025318	118,642594	*1413,5*
r= 0,05	0,00010609	0,00023639	0,00010086	0,00013553	201,19792	*1667*
r= 0,06	1,902E-05	4,376E-05	1,8781E-05	2,4979E-05	205,69372	*1671*
r= 0,07	3,0114E-06	6,5359E-06	2,957E-06	3,5789E-06	183,910959	*2781,5*
r= 0,08	4,8493E-07	1,0125E-06	4,5429E-07	5,5817E-07	180,341325	*2796*
r= 0,09	2,2292E-07	5,4998E-07	2,3932E-07	3,1065E-07	217,643084	*1685,5*
r= 0,1	6,4343E-08	1,615E-07	7,0546E-08	9,095E-08	221,877067	*1691,5*
r= 0,2	5,9807E-11	1,933E-10	8,8956E-11	1,0714E-10	296,467881	*1771,5*
r= 0,3	5,1338E-11	2,3865E-10	1,11E-10	1,2733E-10	411,251743	*1796,5*
r= 0,4	6,0343E-10	3,6962E-09	1,7446E-09	1,9519E-09	534,222741	*1766,5*
r= 0,5	7,869E-09	6,0821E-08	2,8966E-08	3,1854E-08	663,389533	*1730*
r= 0,6	5,5413E-08	5,2174E-07	2,5013E-07	2,7161E-07	798,9566	*1703,5*
r= 0,7	1,9902E-07	2,2084E-06	1,0636E-06	1,1448E-06	934,652298	*1686*
r= 0,8	4,0472E-07	5,1389E-06	2,4826E-06	2,6563E-06	1066,7622	*1675,5*
r= 0,9	5,2906E-07	7,5145E-06	3,6385E-06	3,876E-06	1194,05913	*1670,5*

Table VI: Time at which the number of carcasses fall below 0,001 for different carcass removal rates starting at t=1030 (BetaE=0,0008)

	Number of carcasses	**Infected population**	**Number of infected adults**	**Number of infected piglets**	**Total population**	***Time in days***
r= 0,01	0,0009964	0,00150307	0,00064103	0,00086205	111,325646	*2397*
r= 0,02	0,00099198	0,00170579	0,00072795	0,00097784	116,927921	*2383,5*
r= 0,03	-	-	-	-	-	-
r= 0,04	0,00099823	0,00132709	0,00038257	0,00094453	98,62734	*1324,5*
r= 0,05	0,00099553	0,00168451	0,00047669	0,00120781	95,8914437	*1301,5*
r= 0,06	0,00097773	0,00185431	0,00051789	0,00133643	94,52929	*1287,5*
r= 0,07	0,0009909	0,00197991	0,0005497	0,00143021	93,5568736	*1277*
r= 0,08	0,00097752	0,00201357	0,00056221	0,00145137	92,9835151	*1269,5*
r= 0,09	0,00097152	0,00205248	0,00058111	0,00147137	92,590149	*1263,5*
r= 0,1	0,0009768	0,00211794	0,00061212	0,00150582	92,3424624	*1258,5*
r= 0,2	0,0009895	0,00323137	0,00124026	0,0019911	101,809477	*1241*
r= 0,3	0,00097482	0,00470769	0,00208712	0,00262057	136,244264	*1246*
r= 0,4	0,00099317	0,00643907	0,00303124	0,00340782	192,029154	*1255,5*
r= 0,5	0,00098599	0,00799403	0,00386824	0,00412579	262,046462	*1265,5*
r= 0,6	0,00098125	0,00946163	0,00464405	0,00481757	338,363597	*1273,5*
r= 0,7	0,00098165	0,01090486	0,00539824	0,00550662	414,190756	*1278,5*
r= 0,8	0,00099713	0,01251136	0,00623161	0,00627975	484,311464	*1280*
r= 0,9	0,00098357	0,01374715	0,00688189	0,00686526	547,077791	*1279,5*

Carcass removal at t=1180

Table VII: Lowest number of wild boar for different carcass removal rates starting at t=1180 (BetaE=0,0008)

	Total population	Susceptible population	Number of suscepible adults	Number of susceptible piglets	Infected population	Number of infected adults	Number of infected piglets	Recovered population	Number of recovered adults	Number of recovered piglets	Number of carcasses	*Time in days*
No carcass removal	35,297179	21,706535	7,2149361	14,491598	1,3926054	0,5479132	0,8446922	12,198039	10,711139	1,4869001	3,009889	*3054,5*
r= 0,01	32,1766489	16,1475967	5,1021967	11,5283305	1,40669806	0,49529194	0,91140612	14,6223542	12,3730448	2,24930947	5,1021967	*2998*
r= 0,02	45,2358197	30,9059984	1,74506991	19,2966774	1,61652676	0,72581191	0,89071485	12,7132945	10,5743835	2,13891095	1,74506991	*3438,5*
r= 0,03	58,3981253	6,1885723	42,9000584	5,96326163	3,26632478	0,25787414	3,00845065	48,9432282	34,3709556	14,5722726	42,9000584	*1169,5*
r= 0,04	58,3981253	6,1885723	42,9000584	5,96326163	3,26632478	0,25787414	3,00845065	48,9432282	34,3709556	14,5722726	42,9000584	*1169,5*
r= 0,05	39,1485495	16,1609315	3,10773509	11,7410465	1,66565763	0,69926186	0,96639577	21,3219603	15,9879066	5,33405377	3,10773509	*3370*
r= 0,06	49,3621082	24,6198779	1,4724722	16,635572	1,92759958	0,90834478	1,01925481	22,8146307	16,8313646	5,9832661	1,4724722	*3437,5*
r= 0,07	54,9985361	23,2817552	2,47338264	16,8065332	2,38775689	1,04373693	1,34401996	29,329024	22,4614053	6,86761869	2,47338264	*2304,5*
r= 0,08	58,3981253	6,1885723	42,9000584	5,96326163	3,26632478	0,25787414	3,00845065	48,9432282	34,3709556	14,5722726	42,9000584	*1169,5*
r= 0,09	58,3981253	6,1885723	42,9000584	5,96326163	3,26632478	0,25787414	3,00845065	48,9432282	34,3709556	14,5722726	42,9000584	*1169,5*
r= 0,1	58,3981253	6,1885723	42,9000584	5,96326163	3,26632478	0,25787414	3,00845065	48,9432282	34,3709556	14,5722726	42,9000584	*1169,5*
r= 0,2	58,3981253	6,1885723	42,9000584	5,96326163	3,26632478	0,25787414	3,00845065	48,9432282	34,3709556	14,5722726	42,9000584	*1169,5*
r= 0,3	58,3981253	6,1885723	42,9000584	5,96326163	3,26632478	0,25787414	3,00845065	48,9432282	34,3709556	14,5722726	42,9000584	*1169,5*
r= 0,4	58,3981253	6,1885723	42,9000584	5,96326163	3,26632478	0,25787414	3,00845065	48,9432282	34,3709556	14,5722726	42,9000584	*1169,5*
r= 0,5	58,3982335	6,18990458	42,8871934	5,96450318	3,26605812	0,25784853	3,00820959	48,9422708	34,3710504	14,5712204	42,8871934	*1169,5*
r= 0,6	58,3982335	6,18990458	42,8871934	5,96450318	3,26605812	0,25784853	3,00820959	48,9422708	34,3710504	14,5712204	42,8871934	*1169,5*
r= 0,7	58,3982335	6,18990458	42,8871934	5,96450318	3,26605812	0,25784853	3,00820959	48,9422708	34,3710504	14,5712204	42,8871934	*1169,5*
r= 0,8	58,3982335	6,18990458	42,8871934	5,96450318	3,26605812	0,25784853	3,00820959	48,9422708	34,3710504	14,5712204	42,8871934	*1169,5*
r= 0,9	58,3982335	6,18990458	42,8871934	5,96450318	3,26605812	0,25784853	3,00820959	48,9422708	34,3710504	14,5712204	42,8871934	*1169,5*

Table VIII: Lowest number of carcasses for different carcass removal rates starting at t=1180 (BetaE=0,0008)

	Number of carcasses	Infected population	Number of infected adults	Number of infected piglets	Total population	*Time in days*
No carcass removal	0,00312902	0,003435957	0,0015640	0,0018720	88,999211	*3516,5*
r= 0,01	6,2302E-05	6,9798E-05	3,158E-05	3,8217E-05	92,5644784	*3524,5*
r= 0,02	0,00342217	0,00252438	0,0007009	0,00182348	97,6491191	*1403,5*
r= 0,03	0,00087606	0,00162818	0,00067228	0,0009559	169,795166	*1672*
r= 0,04	0,00012943	0,00024623	0,00010229	0,00014393	172,428389	*1677,5*
r= 0,05	6,6782E-06	1,2333E-05	5,546E-06	6,7866E-06	156,358638	*2784*
r= 0,06	9,4484E-07	1,6679E-06	7,4256E-07	9,2537E-07	152,967887	*2799*
r= 0,07	8,5456E-07	1,5152E-06	6,7058E-07	8,4464E-07	156,932194	*2810,5*
r= 0,08	2,1364E-07	4,3175E-07	1,83E-07	2,4875E-07	184,371918	*1706*
r= 0,09	5,6272E-08	1,153E-07	4,9098E-08	6,6197E-08	188,376683	*1716*
r= 0,1	1,6102E-08	3,3578E-08	1,437E-08	1,9207E-08	193,001402	*1727,5*
r= 0,2	1,5184E-13	8,6668E-13	3,0549E-13	3,4392E-13	359,92195	*2036,5*
r= 0,3	-7,596E-13	1,3806E-12	5,2371E-13	6,4082E-13	606,694909	*2297*
r= 0,4	-9,705E-13	1,2294E-12	4,5361E-13	5,577E-13	654,671977	*2334,5*
r= 0,5	-2,932E-16	5,568E-14	6,4567E-16	7,3684E-16	1316,54022	*2813*
r= 0,6	-1,637E-15	6,8503E-14	7,6477E-15	8,5241E-15	1316,80444	*2944,5*
r= 0,7	-5,602E-06	-5,995E-05	-2,891E-05	-3,104E-05	1316,8068	*3650*
r= 0,8	-3,435E-15	5,7719E-14	1,8674E-15	2,1955E-15	1316,80673	*3115*
r= 0,9	-3,548E-15	5,651E-14	1,6499E-15	1,9601E-15	1312,08358	*2732,5*

Table IX: Time at which the number of carcasses fall below 0,001 for different carcass removal rates starting at t=1030 (BetaE=0,0008)

	Number of carcasses	Infected population	Number of infected adults	Number of infected piglets	Total population	*Time in days*
r= 0,01	0,00099904	0,00073885	0,00030899	0,00042986	70,167077	*3386*
r= 0,02	-	-	-	-	-	-
r= 0,03	0,00099563	0,00197635	0,00080585	0,0011705	162,8096	*1651*
r= 0,04	0,00099384	0,00091133	0,00024537	0,00066596	92,3400072	*1373*
r= 0,05	0,00098999	0,00110108	0,0002915	0,00080958	87,8288272	*1349*
r= 0,06	0,00099726	0,00132367	0,00034995	0,00097372	85,3081189	*1335*
r= 0,07	0,00099489	0,00153157	0,00040535	0,00112622	83,645788	*1325,5*
r= 0,08	0,00098503	0,00171555	0,00045485	0,0012607	82,445371	*1318,5*
r= 0,09	0,00099701	0,00193435	0,00051321	0,00142114	81,415322	*1312,5*
r= 0,1	0,0009888	0,00209884	0,00055803	0,0015408	80,6591332	*1308*
r= 0,2	0,00099207	0,00362247	0,00098005	0,00264242	76,8071487	*1285*
r= 0,3	0,00096791	0,00485779	0,00132317	0,00353462	75,2899514	*1276*
r= 0,4	0,0009892	0,00629885	0,00170618	0,00459268	74,2386868	*1270*
r= 0,5	0,00098665	0,00761801	0,00204865	0,00556935	73,5295534	*1266*
r= 0,6	0,00097782	0,00887914	0,00236882	0,00651032	72,9901309	*1263*
r= 0,7	0,00097431	0,01017531	0,00269055	0,00748476	72,5336845	*1260,5*
r= 0,8	0,00099872	0,01178876	0,00308048	0,00870828	72,0668688	*1258*
r= 0,9	0,00097331	0,01282744	0,00333055	0,00949689	71,7918205	*1256,5*

Annex 3: Outbreak with culling

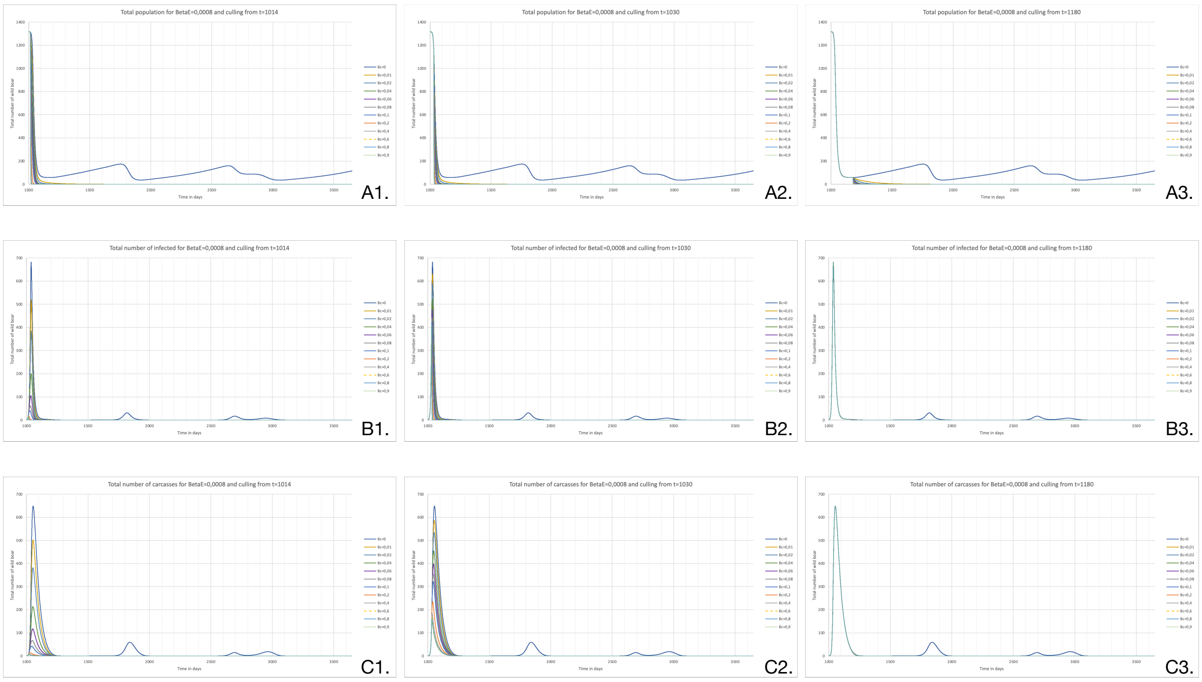


Figure IV: The course of the disease after ASF is introduced at a 1000 days for different culling rates (*bc*) and a carcass transmission rate (*BetaE*) of 0,008. **A**.: The total population wild boar for culling from day 1014 (*A1.*), day 1030 (*A2.*) and day 1180 (*A3.*); **B**.: The number of infected for culling from day 1014 (*B1.*), day 1030 (*B2.*) and day 1180 (*B3.*); **C**. The number of carcasses for culling from day 1014 (*C1.*), day 1030 (*C2.*) and day 1180 (*C3.*)

Annex 4: Outbreak with wolf

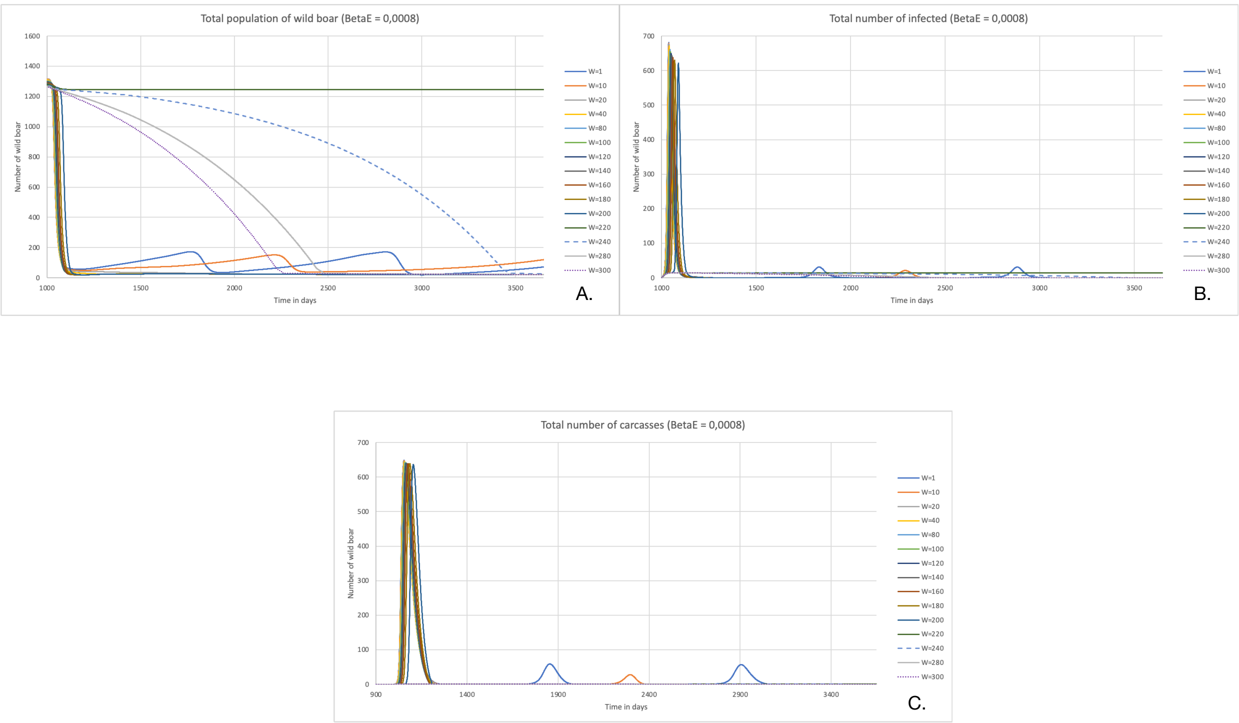
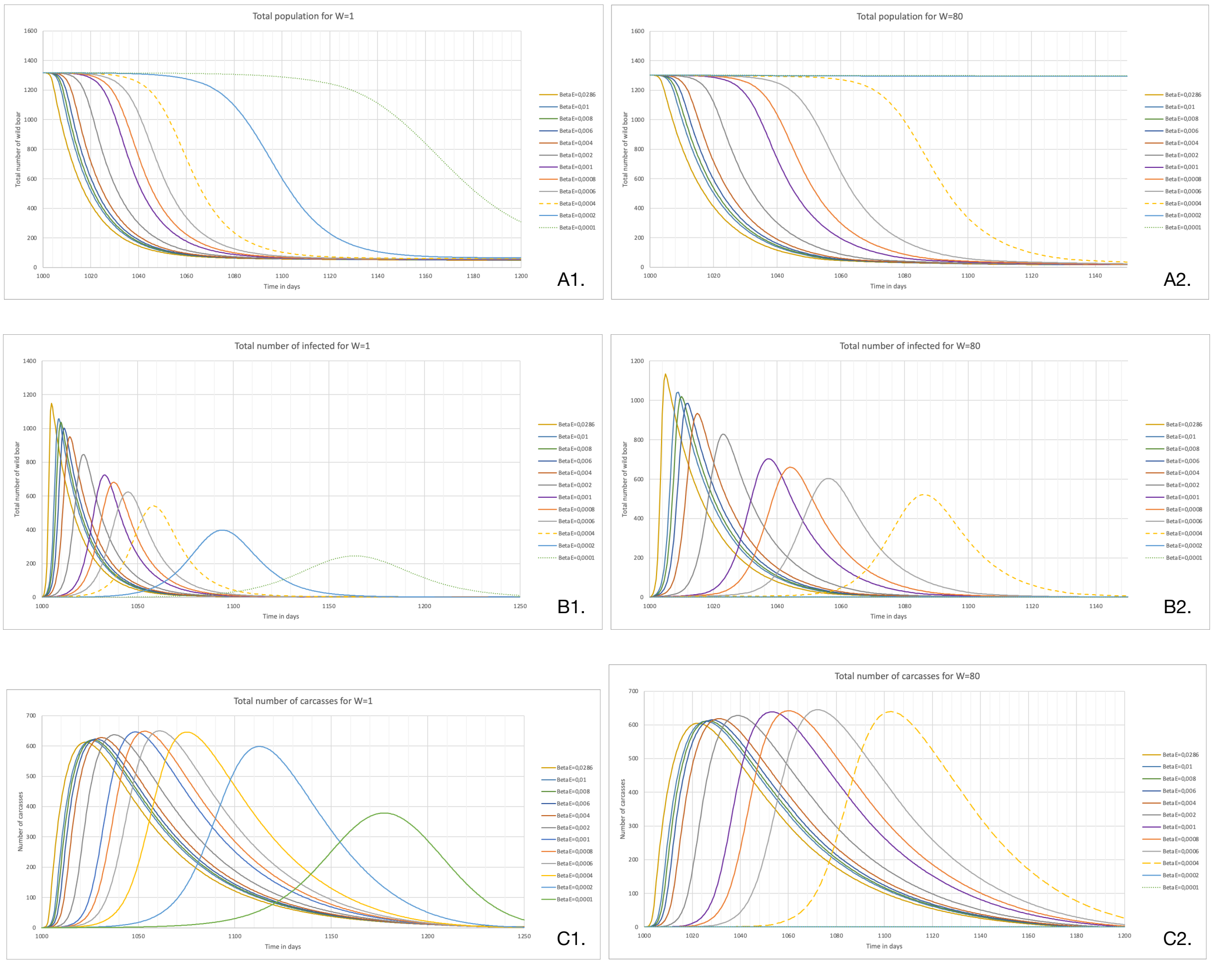


Figure V: The course of the initial ASF outbreak for different numbers of wolves (*W*) and a carcass transmission rate (*BetaE*) of 0,0008.; **A**.: The total population wild boar.; **B**.: The total number of infected.; **C**. The total number of carcasses.



A1. A2. B1. B2. C1. C2.

Figure VI: The comparative effect of 1 and 80 wolves (*W*) and different carcass transmission rates (*BetaE*) on the course of the initial outbreak. The outbreak occurs later for a lower carcass transmission rate and a smaller number of wolves. If 80 wolves are present, an equilibrium seems to be reached for a carcass transmission rate of 0,0002 and 0,0001.

Annex 5: Outbreak with wolf and carcass removal

Carcass removal at t=1014

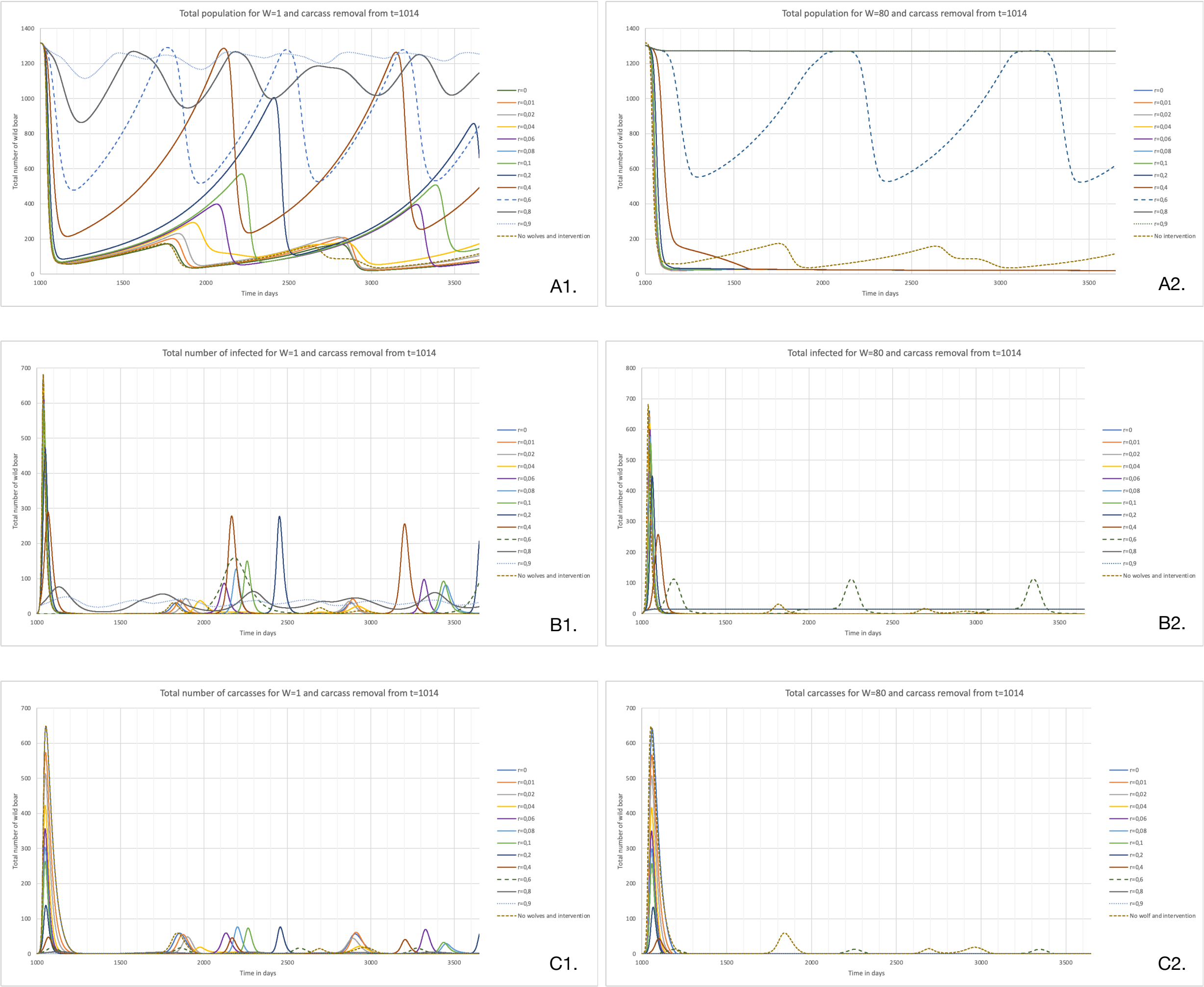


Fig. VII: The course of the initial ASF outbreak for different numbers of wolves (*W*) and carcass removal rates (*r*). Carcass removal was started at day 1014 and the carcass transmission rate was 0,0008.; **A**.: The total population wild boar for 1 wolf (*A1.*) and 80 wolves (*A2.*).; **B**.: The number of infected for 1 wolf (*B1.*) and 80 wolves (*B2.*).; **C**. The number of carcasses for 1 wolf (*C1.*) and 80 wolves (*C2.*).

Carcass removal at t=1030

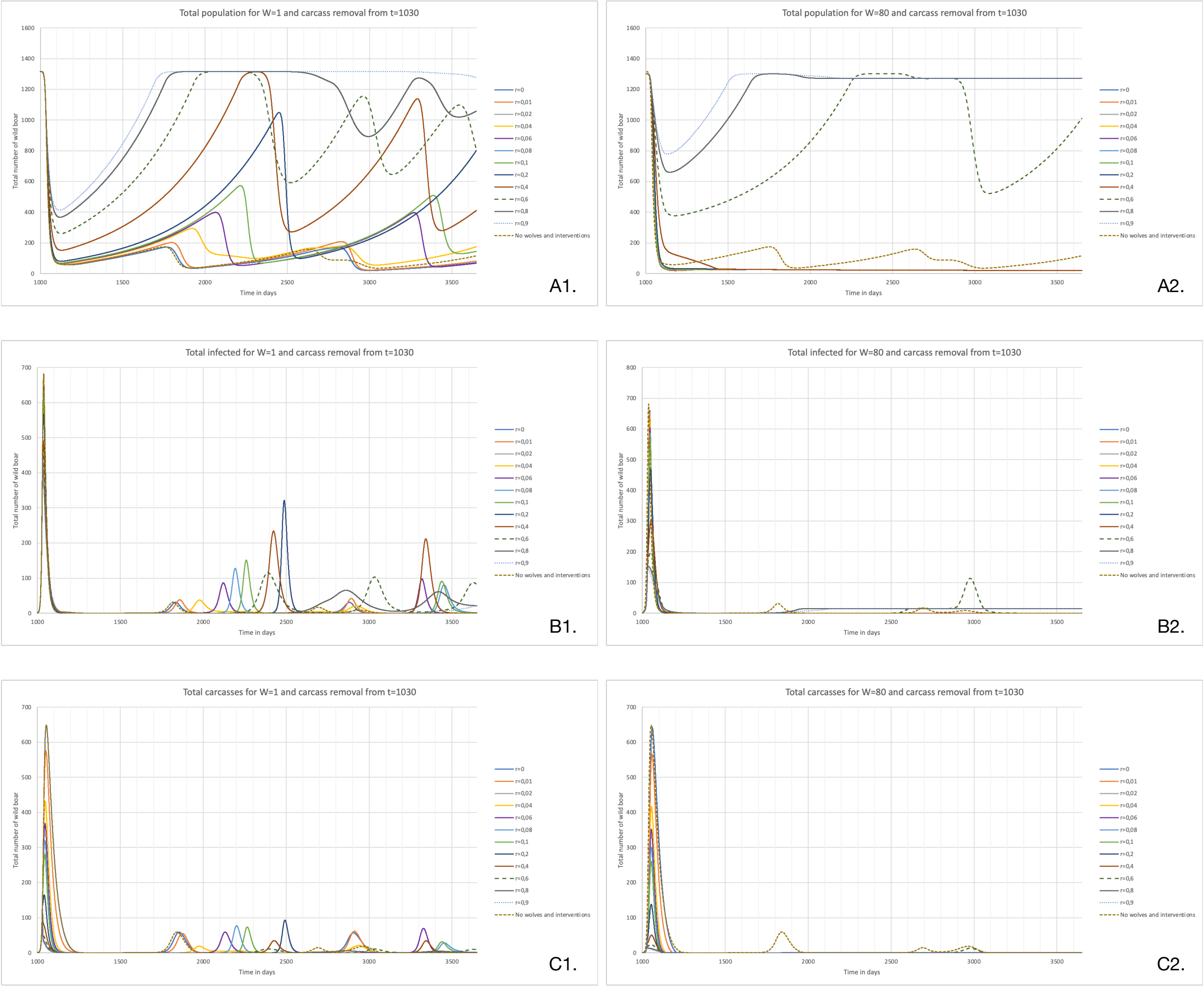


Fig. VIII: The course of the initial ASF outbreak for different numbers of wolves (*W*) and carcass removal rates (*r*). Carcass removal was started at day 1030 and the carcass transmission rate was 0,0008.; **A**.: The total population wild boar for 1 wolf (*A1.*) and 80 wolves (*A2.*).; **B**.: The number of infected for 1 wolf (*B1.*) and 80 wolves (*B2.*).; **C**. The number of carcasses for 1 wolf (*C1.*) and 80 wolves (*C2.*).

Carcass removal at t=1180

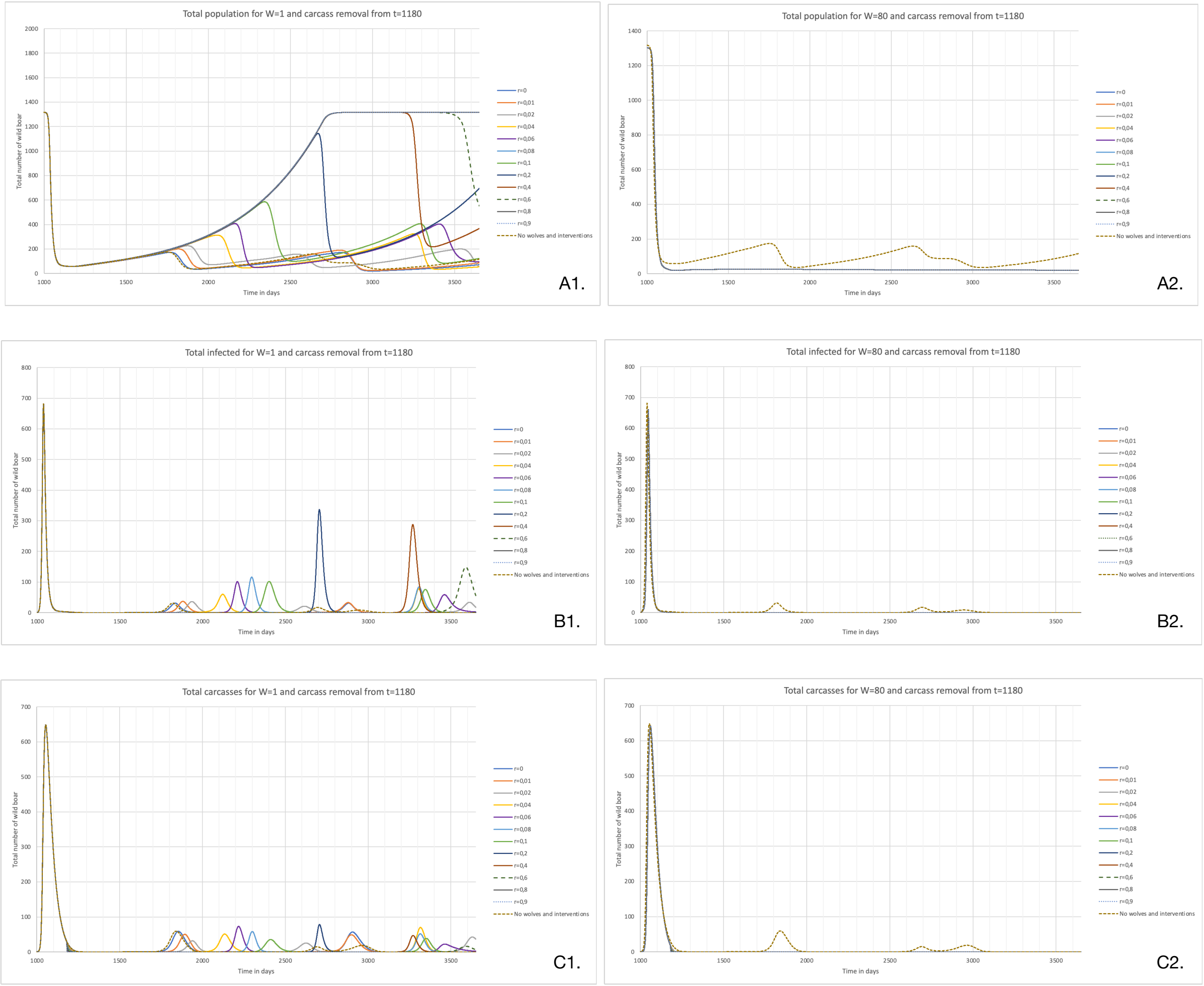


Fig. IX: The course of the initial ASF outbreak for different numbers of wolves (*W*) and carcass removal rates (*r*). Carcass removal was started at day 1180 and the carcass transmission rate was 0,0008.; **A**.: The total population wild boar for 1 wolf (*A1.*) and 80 wolves (*A2.*).; **B**.: The number of infected for 1 wolf (*B1.*) and 80 wolves (*B2.*).; **C**. The number of carcasses for 1 wolf (*C1.*) and 80 wolves (*C2.*).

Annex 7: Outbreak with culling and carcass removal

Carcass removal & culling at t=1014

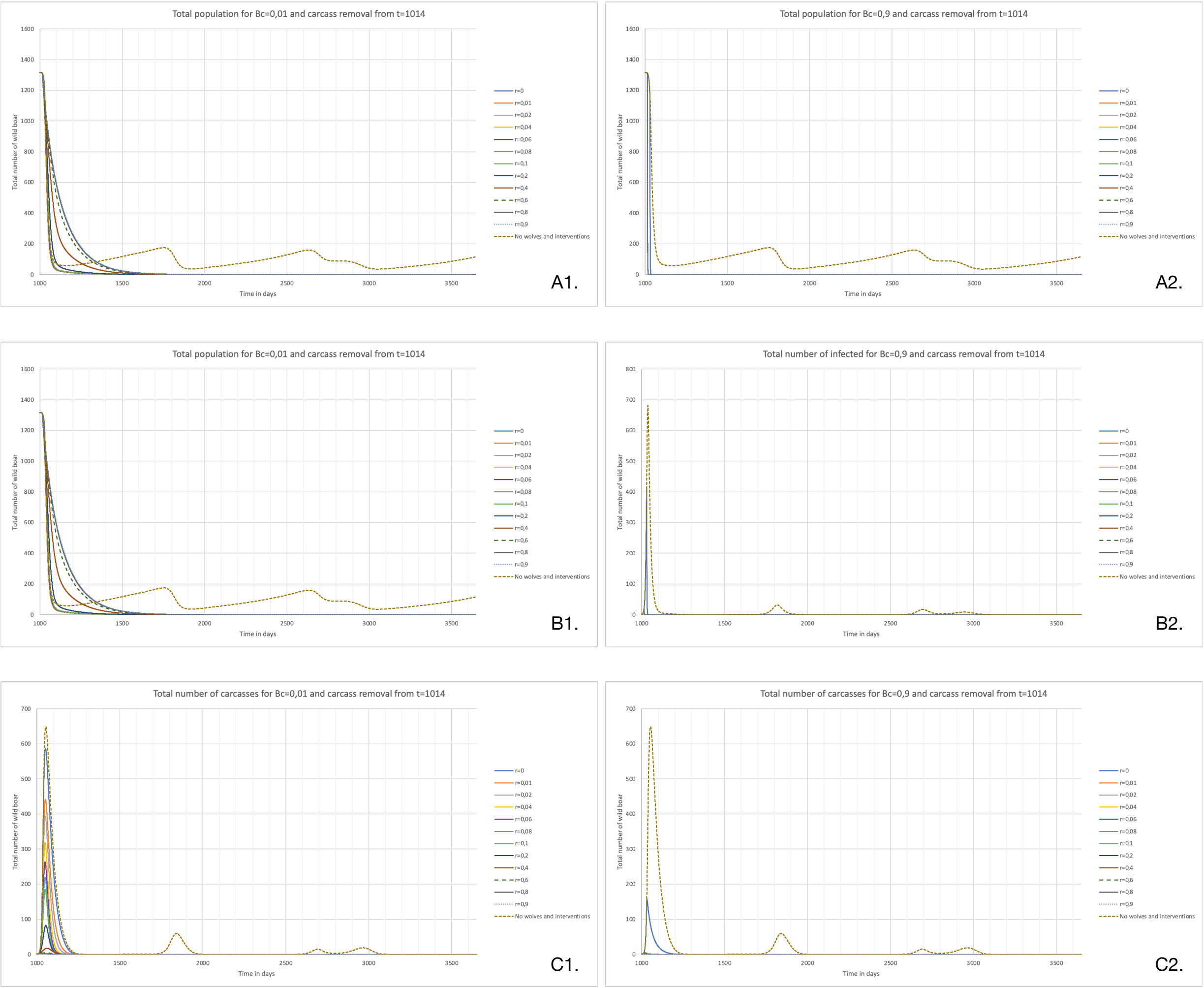


Figure X: The course of the initial ASF outbreak for different carcass removal rates (*r*) and culling rates (*bc*). Carcass removal and culling was started at day 1014 and the carcass transmission rate was 0,0008.; **A**.: The total population wild boar for a culling rate of 0,01 (*A1.*) and 0,9 (*A2.*).; **B**.: The number of infected for a culling rate of 0,01 (*B1.*) and 0,9 (*B2.*).; **C**. The number of carcasses for a culling rate of 0,01 (*C1.*) and 0,9 (*C2.*).

Carcass removal & culling at t=1030

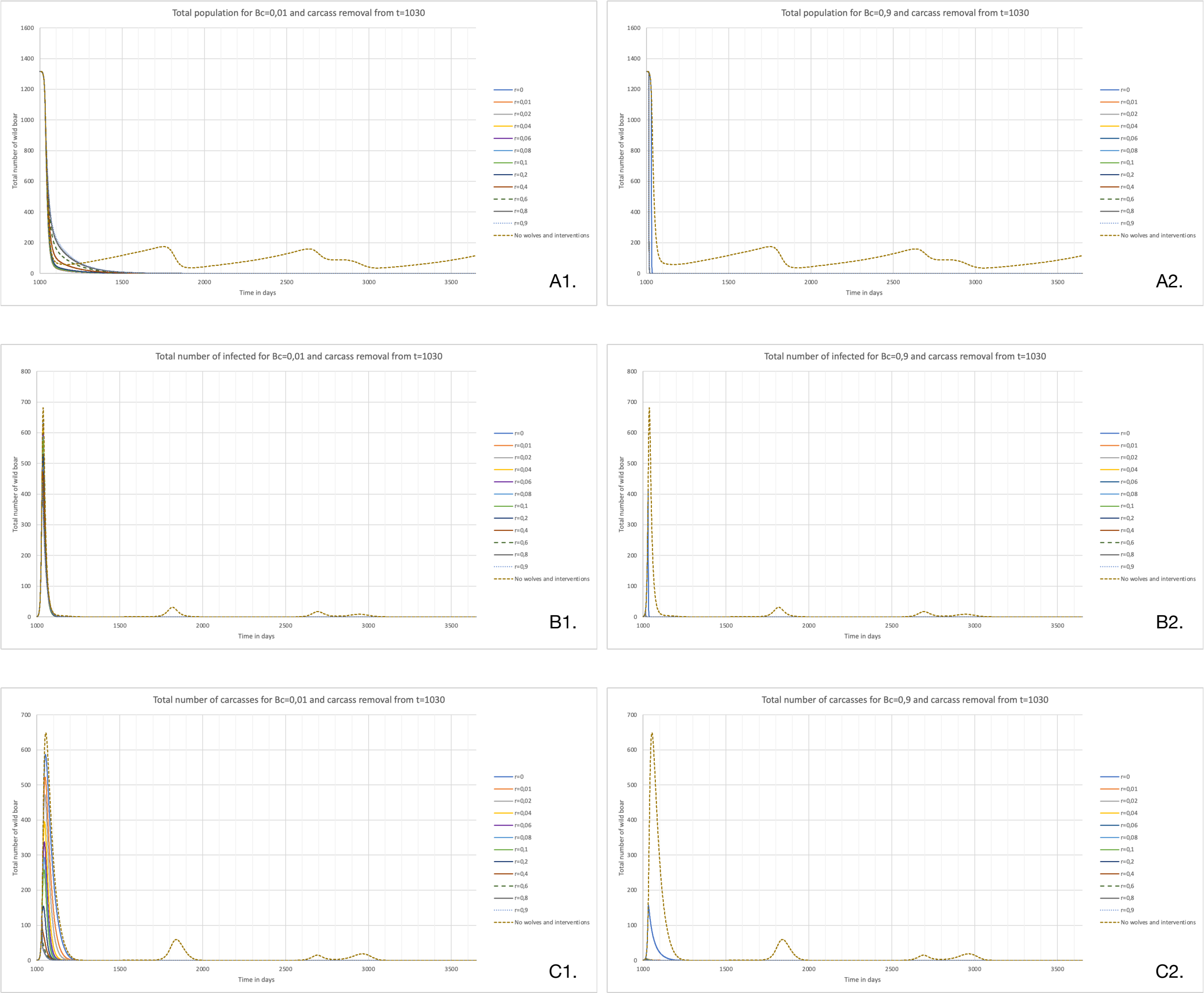


Figure XI: The course of the initial ASF outbreak for different carcass removal rates (*r*) and culling rates (*bc*). Carcass removal and culling was started at day 1030 and the carcass transmission rate was 0,0008.; **A**.: The total population wild boar for a culling rate of 0,01 (*A1.*) and 0,9 (*A2.*).; **B**.: The number of infected for a culling rate of 0,01 (*B1.*) and 0,9 (*B2.*).; **C**. The number of carcasses for a culling rate of 0,01 (*C1.*) and 0,9 (*C2.*).

Carcass removal & culling at t=1180

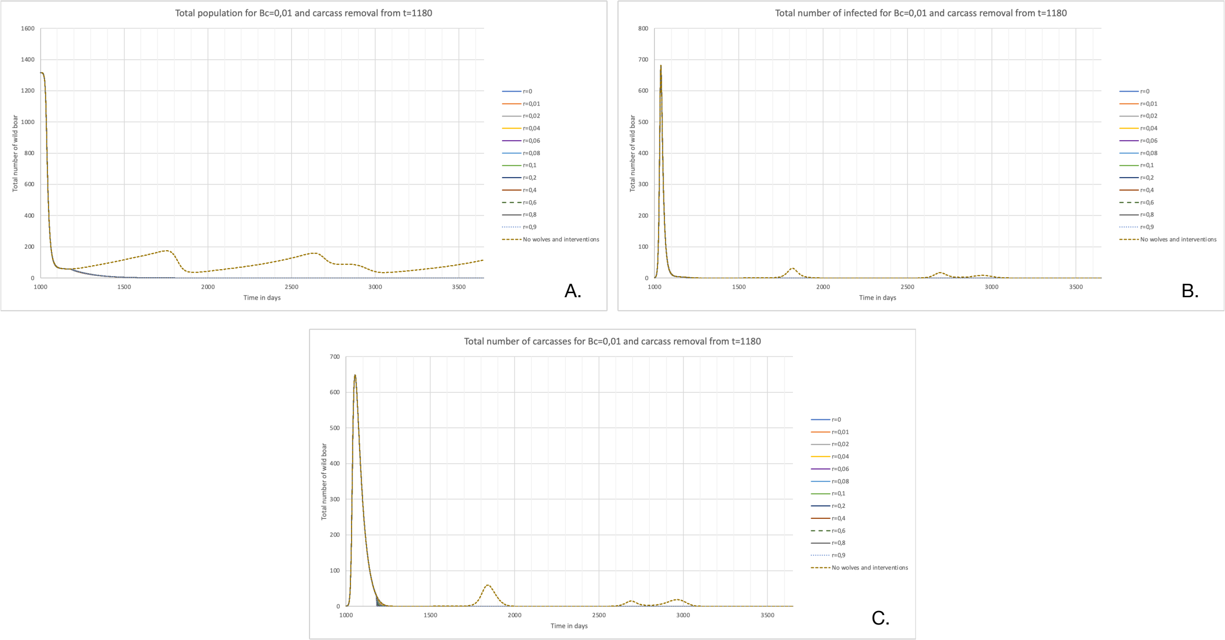


Figure XII: The course of the initial ASF outbreak for different carcass removal rates (*r*) and a culling rate (*bc*) of 0,01. Carcass removal and culling was started at day 1180 and the carcass transmission rate was 0,0008.; **A**.: The total population wild boar for a culling rate of 0,01; **B**.: The number of infected for a culling rate of 0,01; **C**. The number of carcasses for a culling rate of 0,01.

Annex 7: Outbreak with wolf and culling

Culling from t=1014

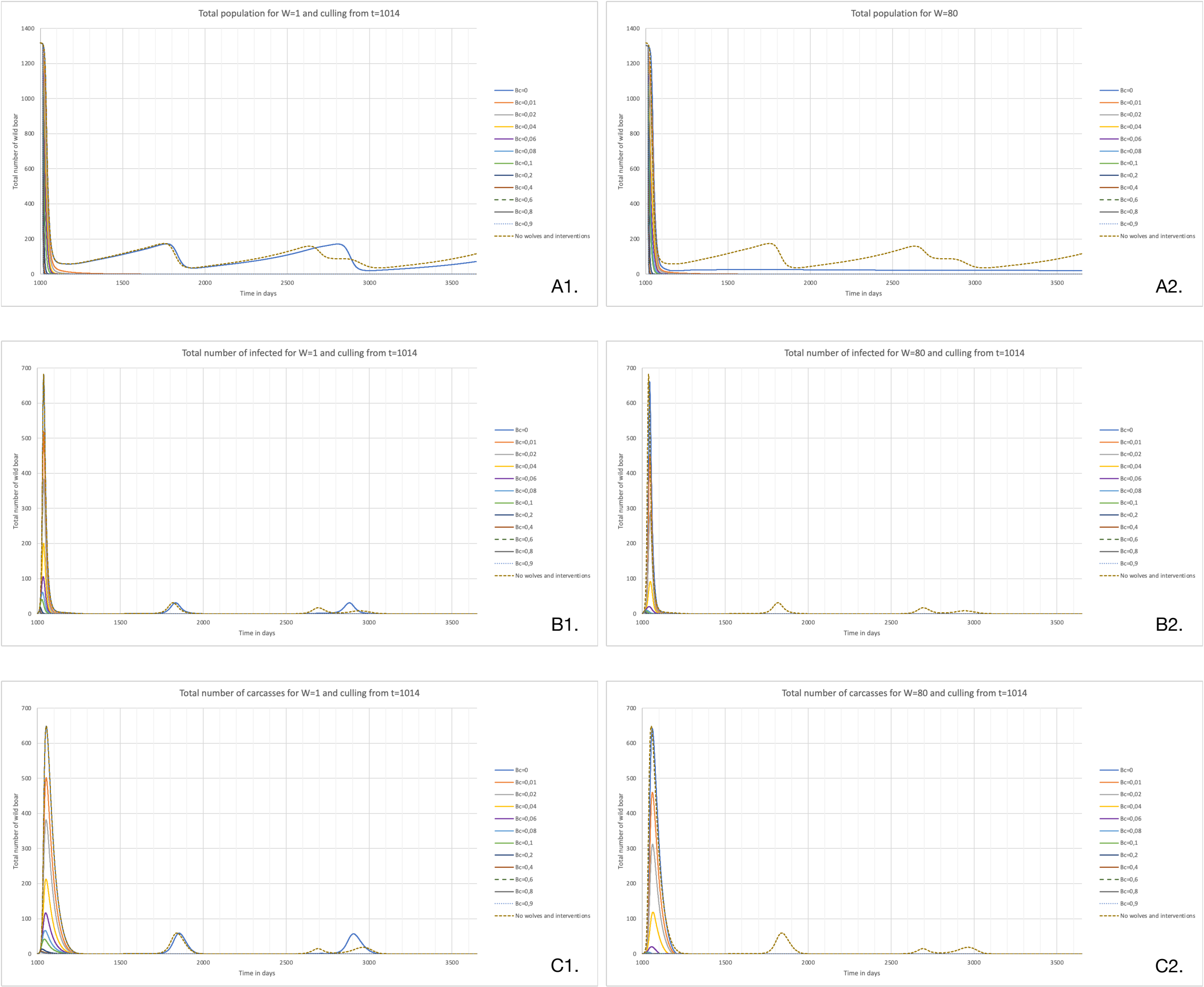


Fig. XIII: The course of the initial ASF outbreak for different numbers of wolves (*W*) and culling rates (*bc*). Culling was started at day 1014 and the carcass transmission rate was 0,0008.; **A.**: The total population wild boar for 1 wolf (*A1.*) and 80 wolves (*A2.*).; **B.**: The number of infected for 1 wolf (*B1.*) and 80 wolves (*B2.*).; **C**. The number of carcasses for 1 wolf (*C1.*) and 80 wolves (*C2.*).

Culling at t=1030

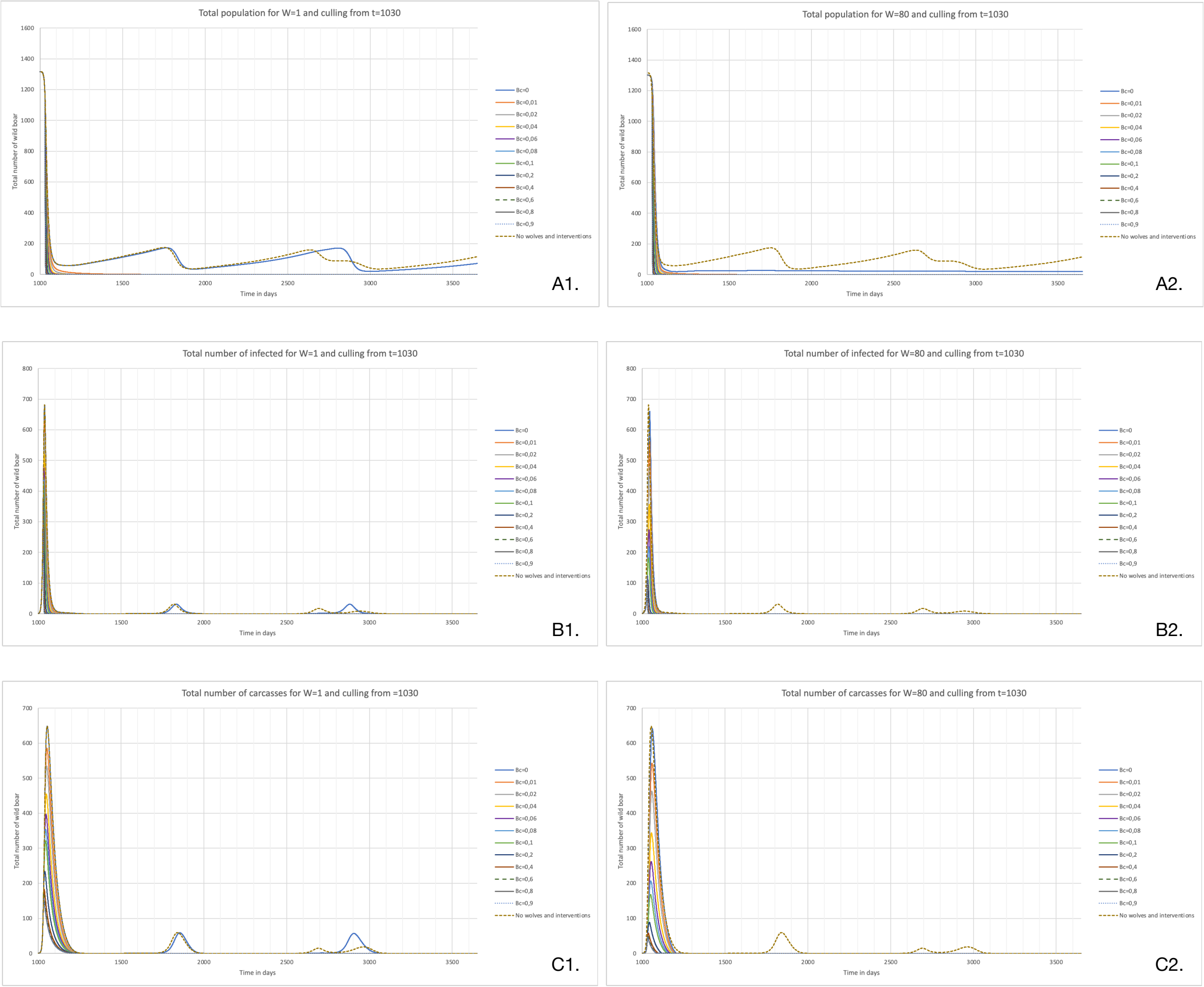


Fig. **XIV**: The course of the initial ASF outbreak for different numbers of wolves (*W*) and culling rates (*bc*). Culling was started at day 1030 and the carcass transmission rate was 0,0008.; **A**.: The total population wild boar for 1 wolf (*A1.*) and 80 wolves (*A2.*).; **B**.: The number of infected for 1 wolf (*B1.*) and 80 wolves (*B2.*).; **C**. The number of carcasses for 1 wolf (*C1.*) and 80 wolves (*C2.*).

Culling at t=1180

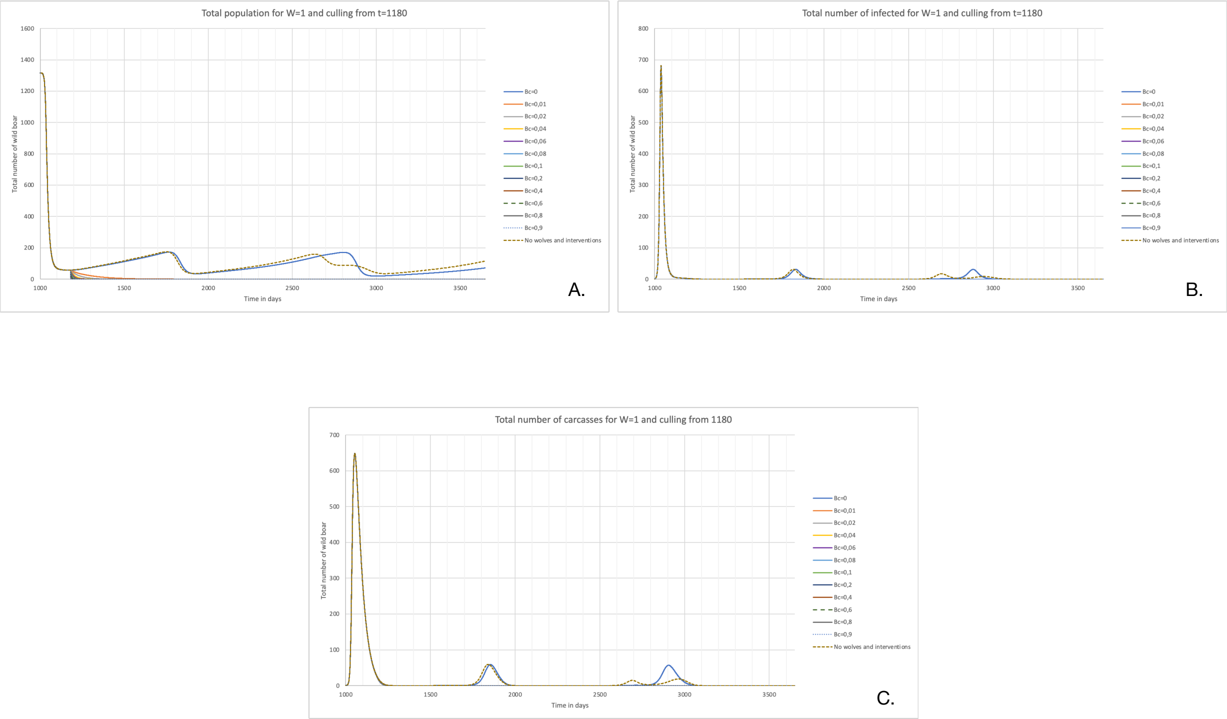


Fig. XV: The course of the initial ASF outbreak for different culling rates (*bc*) and 1 wolf (*W*). Culling was started at day 1180 and the carcass transmission rate was 0,0008.; **A**.: The total population wild boar for 1 wolf; **B**.: The number of infected for 1 wolf; **C**. The number of carcasses for 1 wolf.