Could African Swine Fever persist in the feral pig population in Scotland?
- Descriptive analysis and individual-based stochastic ASF modelling of the Scottish feral pig population.

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Abstract

African swine fever (ASF) represents a major global threat to the pig industry, and the maintenance and spread of infection via wild boar complicates its control. In Scotland, ASF preparedness is also an urgent concern, yet the potential role of feral pigs remains poorly understood due to limited and fragmented data. This study therefore aimed to: (1) compile and evaluate existing data on feral pigs in Scotland; (2) investigate interactions between feral and outdoor-reared domestic pigs; and (3) model ASF infection dynamics in feral pigs, including persistence, to inform risk assessment and management strategies.

Chapter 1 revealed substantial gaps in the availability and quality of feral pig distribution and abundance data, highlighting the difficulty of obtaining accurate population estimates and the urgent need for systematic monitoring. Chapter 2 provided preliminary evidence and quantitative estimates of interactions between feral and outdoor-reared domestic pigs, including exploratory and aggressive behaviours, suggesting that official records may underestimate the distribution of feral pigs and that groups of feral pigs were observed entering farms simultaneously, representing a non-negligible risk for ASF transmission. Chapter 3 developed a simulation model of ASF in feral pig populations in Dumfries and Galloway, which indicated that ASF can persist even at very low population densities, with early between-group transmission and carcass-mediated infection being key drivers of persistence. Incorporating survey data from Chapter 2 suggested the range of possible interpretations for farm-based detection probabilities and the actual frequency of visits by feral pigs, in line with the reported data.

Integrating these findings provides a comprehensive understanding of ASF risk in Scotland. Effective management requires reliable data collection, risk-based surveillance, rapid containment, and removal of infectious carcasses. This study illustrates the complex interplay between feral pig ecology, farm management, and disease dynamics, offering important insights for contingency planning and the prioritisation of biosecurity measures.

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Acknowledgement

My time conducting this research has been deeply rewarding.

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I would like to express my deepest gratitude to my husband Hikaru, who took parental leave to come with me to the UK and devoted himself to raising our children in an unfamiliar environment; my daughter Rena, who has accompanied me patiently since infancy; and my daughter Nanoha, who was safely born after our return to Japan. I also owe a special debt of gratitude to my parents in Japan for their unwavering support. Without all of their support, this journey would not have been possible.

Through this research, I have not only gained knowledge and analytical skills, as well as the experience of adopting a fact-based, neutral stance as a provider of scientific evidence, but also perseverance and the invaluable experience of living and conducting research abroad. I would also like to thank the warm and supportive staff at MVLS, as well as the friendly and welcoming people of Glasgow.

I am determined to apply these experiences to my future work, contributing to animal health globally—including in Japan and the UK—and to the promotion of One Health.

Finally, I sincerely hope that this study will help inform ASF contingency planning in Scotland and support future research in this field.

Author's Declaration

I declare that, except where explicit reference is made to the contribution of others, this thesis is the result of my own work and has not been submitted for any other degree or professional qualification at the University of Glasgow or any other institution.

Chapter 1 Introduction

Wildlife-livestock interface

Pathogen-sharing at the wildlife-livestock interface is a growing global issue of concern (Gortázar et al., 2007). Pathogens shared by livestock and wild animals pose multidisciplinary problems, including public health, economic losses, wildlife conservation and animal welfare (Gortázar et al., 2008; Kukielka et al., 2013; Michel et al., 2010; Sainsbury et al., 1995). Infectious diseases in which wildlife-livestock interactions play an important role include avian influenza, foot-and-mouth disease and African swine fever (ASF) (Jori et al., 2021), all of which are livestock diseases of very high priority, and some are also zoonoses. Wild animals may not only be infected by livestock pathogens and spill back to livestock but also be long-range disease carriers, as a result of wildlife movements (Calisher et al., 2006; Conner et al., 2008; Smith et al., 1996). For example, in ASF currently circulating in Europe, the possibility of transboundary ASFV transmission by wild boar has been reported (Sauter-Louis et al., 2021). Considering the animal-wildlife interface is a necessary part of effective control of emerging animal diseases (Ezanno et al., 2022). Nevertheless, for many pathogens, the epidemiological role of wildlife in infectious disease transmission remains largely unknown (Martin et al., 2011).

African Swine Fever (ASF)

African swine fever (ASF), caused by the African swine fever virus (ASFV) (Blome et al., 2013; de Carvalho Ferreira et al., 2013), is a highly lethal disease affecting both domestic pigs and wild boar. It is classified as a notifiable disease under international and UK regulations, due to its high mortality, absence of effective vaccines or treatments, and substantial socio-economic consequences (Guberti et al., 2019; Niemi, 2020). Originally restricted to sub-Saharan Africa, ASF has emerged over the past decade as a considerable threat to pig production in Europe and Asia (Sauter-Louis et al., 2021). After ASFV was first reported in Georgia in 2007, the disease disseminated to several Eastern European countries, largely via wild boar movements (Taylor et al., 2020). Despite rigorous control measures, ASF has since expanded globally, affecting over 80 countries and regions across Africa, the Americas, Asia, Europe, and Oceania (Penrith, 2020).

In Europe, ASFV has continued to spread steadily westwards. Notably, genotype II ASFV was detected in wild boar in mainland Italy in January 2022 (OIE, 2022; OIE WAHIS, 2022c) and subsequently in Italian domestic pigs in June 2022 (OIE WAHIS, 2022a). Germany confirmed ASFV in domestic pigs for the first time in its western regions in July 2022 (OIE WAHIS, 2022b). These events highlighted the role of both wild boar and human-mediated pathways in disease spread. In response, the UK Department for Environment, Food and Rural Affairs (DEFRA) raised the assessed likelihood of ASFV introduction via human-mediated routes from moderate to high in July 2022 (DEFRA, 2022). DEFRA's most recent risk assessments suggest that this heightened level of concern has remained unchanged through 2025, emphasising the continued relevance of ASFV introduction risk to the UK (DEFRA, 2025). The broader geographical context of ASF occurrence is illustrated in Figure 1.

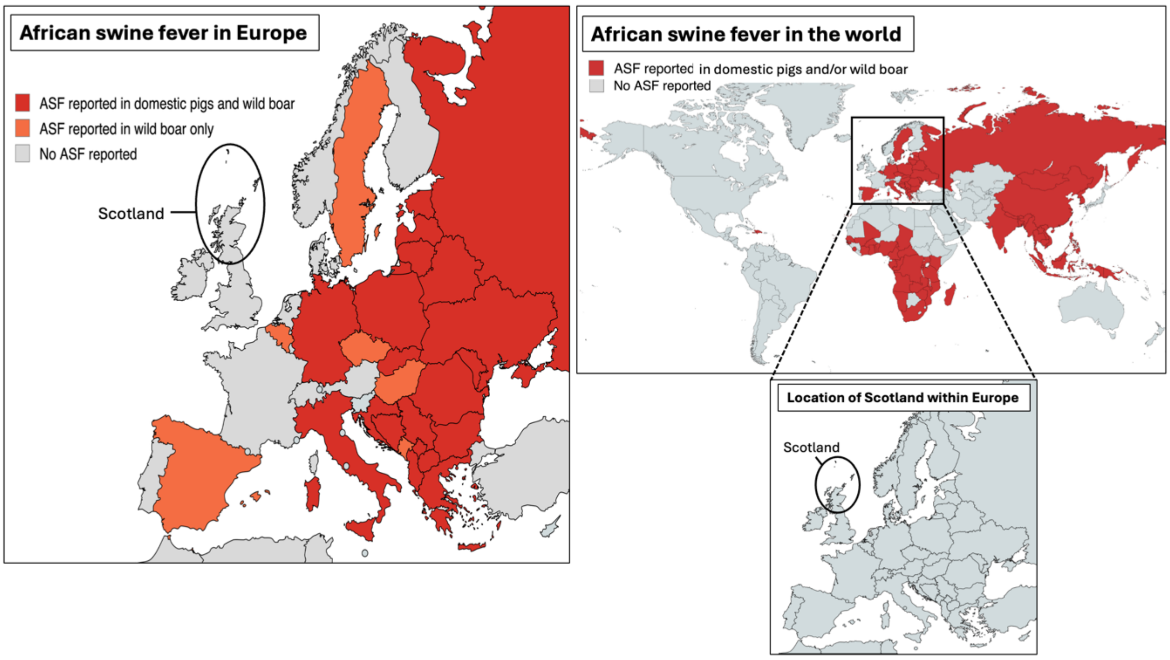

Figure 1. Maps showing the distribution of African swine fever (ASF) in Europe and worldwide, with the location of Scotland highlighted.

In Europe, countries are classified according to whether ASF has been reported in domestic pigs and wild boar, or in wild boar only. At the global level, ASF occurrence is presented more generally due to differences in data availability. These maps provide broader geographical context for the study area. Base map created using MapChart (https://www.mapchart.net), with ASF occurrence data based on reports from WOAH.

Transmission of ASFV

ASFV is primarily transmitted via direct or indirect contact with infected animals (Costard et al., 2013; Guinat et al., 2016). Infected animals begin shedding the virus soon after infection, through saliva, nasal secretions, faeces, and urine (Costard et al., 2013; Guinat et al., 2014, 2016). Susceptible animals may become infected through direct contact, exposure to contaminated carcasses or excreta, consumption of infected meat or meat products, swill feed containing infected material, or contact with contaminated fomites, including clothing, vehicles, and equipment (Olesen et al., 2017; Vilalta, 2018). While ASFV can also be transmitted by soft-bodied Argasid ticks (e.g., Ornithodorus spp.), these vectors are not present in the UK (DEFRA, 2018). The persistence of ASFV in carcasses and the environment, even in the face of high mortality and culling efforts, underlines the importance of indirect transmission routes in maintaining the virus in wild boar populations (Chenais et al., 2018; Pepin et al., 2020).

Recent European outbreaks demonstrate that ASFV can circulate within wild boar populations independently of domestic pigs, sustained through a “boar–habitat cycle” involving both direct contact and indirect transmission via virus-contaminated carcasses and environments (Chenais et al., 2018; Nielsen et al., 2021). The environmental resilience of ASFV—remaining viable in blood for over a year at 4°C, in meat for several months, and in frozen carcasses for several years (Sanchez-Vizcaino et al., 2009)—compounds the challenge of controlling infection in wild populations.

ASF in wild boar/feral pigs

If ASF is introduced into a wild boar population, controlling the infection could be extremely difficult. Since 2007, only the Czech Republic and Belgium achieved ASF-free status following infection of wild boar population (OIE Delegate for Belgium, 2019; OIE Delegate for Czech Republic, 2019). Achieving eradication of ASF in wild boar cost Belgium more than 160 million euros in the two years from the first confirmed case to ASF-free declaration (Heymans, 2021). In addition, a major effort was made to depopulate the wild boar around the infected zone and to erect more than 300 km of boar-proof fences (Heymans, 2021). These experiences illustrate that ASF eradication in wild boar entails substantial logistical and financial challenges. Consequently, preventing ASFV infection in feral pig populations and establishing contingency plans are critical components of preparedness.

Although native wild boar was extirpated from the UK over 700 years ago (Massei & Ward, 2022), populations of feral pigs, originating from escaped farmed boar and illegal releases of hybrids, have become established in recent decades (Wilson, 2014; DEFRA, 2018). The UK government and NatureScot use the term “feral pigs” for these populations to distinguish them from native wild boar. In England, the Forest of Dean supports the largest and best-studied population, with animals that have been monitored since the early 2000s (Massei & Genov, 2004; Massei & Ward, 2022).

In Scotland, there are now at least two to three breeding populations, with sightings reported across multiple regions (Campbell & Hartley, 2010). Feral pigs in Scotland preferentially occupy forested and semi-natural areas but are also observed near agricultural lands, highlighting their adaptability and potential for local spread (Lovell et al., 2024). Dumfries and Galloway, a county in the south-west of Scotland, is believed to have the largest breeding feral pig population in Scotland (Dell, 2020). The area has approximately 350km of coastline and 6,439km^2 of land, of which approximately 35% is covered by forests and woodlands (NatureScot, 2019). The region has a rich natural heritage such as the Galloway Forest Park, the Galloway and Southern Ayrshire Biosphere, and the Galloway Dark Sky Park (NatureScot, 2019). Livestock is the main agricultural industry in the region, with pasture accounting for 88% of the agricultural land (Dell, 2020). Modelling of feral pig population dynamics in Dumfries and Galloway based on NBN records by Dell (2020) estimated that the population in the region would be 7150 pigs occupying an average area of 124 km^2, with the largest population predicted to be in the New Abbey area (Dell, 2020).

Mathematical modelling of ASF

Mathematical modelling is useful for studying complex phenomena such the dynamics of infectious disease pathogens in population (Jong, 1995). It has also played an important role in understanding the epidemiological dynamics in wildlife population (O’Neill et al., 2020). A disease spread model, which represents a simplified real-world disease transmission system, is used to achieve a better understanding of disease transmission dynamics, to predict disease transmission and its impact in population, and to consider effective interventions against transmission (Kirkeby et al., 2021). Since the first publication in 2011, mathematical models of ASFV have been widely used to improve our understanding of the transmission dynamics of ASFV (Hayes et al., 2021). ASF models for wild boar are often individual-based, spatially structured models that incorporate existing information on the demography of the boar (Dankwa et al., 2022). Many ASFV transmission models use the classical Susceptible-Exposed-Infectious-Removed (SEIR) structure (Guinat et al., 2018; Halasa et al., 2019).

The majority of ASFV infection models for wild boar published to date are based on the ASF wild boar model developed by Lange & Thulke (2017). These models simulated disease spread with movement-based algorithms, and most models represented it by clustered spatial habitat grids (e.g., Halasa et al., 2019; Pepin et al., 2021; Salazar et al., 2022).

Simulation in the UK

The UK landscape differs from other ASF-affected European countries where wild boars are widely distributed across large areas of woodland, which could make a significant difference in the course of ASF transmission. The only ASFV simulation in feral pigs in the UK to date has been carried out by Croft et al. They developed a spatially explicit individual-based model for an isolated feral pig population in the Forest of Dean in western England to predict the outcome of ASF (Croft et al., 2020). The UK Forestry Commission owns woodland in the part of Forest of Dean, where population management and, since 2013, annual monitoring of feral pigs has been carried out (Gill, 2022a). The model study site covered a 25 km buffer zone around that area, and in this study, a mosaic of random polygons scaled to the average wild boar herd was used instead of a grid-based landscape to avoid cluster-related biases. The components of feral pigs in the model were parameterised according to the description of Croft et al. (2018) and epidemiological parameters were adopted from Lange and Thulke (2017) . For transmission routes, direct transmission via direct contact with infected cohorts of the same social group and indirect transmission via contact with the carcass were considered. Simulation showed that ASFV was predicted to be highly unlikely to persist long-term in an isolated feral pig population in the Forest of Dean, with a median time of 15 weeks predicted for the disease to fade out.

Simulation in a country without a large wild boar population

Wild boar are key in ASFV transmission and persistence in Europe (Halasa et al., 2019). It has previously been assumed that the population in Scotland is too small to be able to maintain ASF, but with the perception that the population is increasing, this could change. Halasa et al. simulated ASFV transmission in a wild boar population in Denmark, a country with a small wild boar population, using actual landscape data (Halasa et al., 2019). Their model was based on the spatio-temporal and stochastic wild boar population model (Kramer-Schadt et al., 2009b; Lange et al., 2012) and the ASF transmission models (Lange, 2015; Lange & Thulke, 2017). The population composition of wild boar (e.g., the ratio of piglets to adults), was simulated based on Merta et al. (2015) due to the lack of data on Danish wild boar. The simulation predicted that the epidemic would generally last for several months and then burn out. The persistence of the ASF epidemic in Danish wild boar was estimated to depend on the size and location of the boar population. This model was also adapted for ASF simulation in wild boar in France by Salazar et al (Salazar et al., 2022).

The scientific aim of this research project

Despite a perception that increasing number of feral pigs are becoming a problem in Scotland, data on their population, habitat, and interactions with domestic pigs are very limited and not well organised. Furthermore, although ASF infection in feral pigs has the potential to be long-lasting and could have a significant impact on the UK pig industry and socio-economy, the potential for persistence of ASF infection in feral pigs in Scotland has not been investigated.

This study therefore aimed to achieve the following objectives:

Chapter 2 focuses on compiling and evaluating the availability and quality of existing data on Scottish feral pigs, in order to identify knowledge gaps and provide recommendations for future studies.

Chapter 3 investigates potential interactions between feral and domestic pigs in Scotland through a survey to quantitatively estimate the likelihood of interactions that could facilitate ASF transmission.

Chapter 4 develops a simulation model of ASF infection in feral pigs in Dumfries and Galloway to investigate infection dynamics and persistence, incorporating observed data from Chapter 3 to estimate probabilities and inform management strategies.

These results provide important information for decision-making on ASF contingency planning and feral pig management in Scotland, identifying areas for further research.

Roles and responsibilities

Chapter 2 - All aspects of this work, including study design, data collection, analysis, and interpretation, were carried out independently by the author. This research was not part of any collaborative project and represents solely the author's own contribution.

Chapter 3 - In order to achieve the second objective outlined above, the quantification of interactions with domestic pigs was based on responses obtained from a questionnaire survey. These questions were included as part of a wider questionnaire survey, conducted in collaboration with another student, Tahreem Khalid (Université de Lyon). The analysis of responses relating to the quantification of interactions with domestic pigs was conducted entirely independently of that study and represents work carried out solely by the present author.

Chapter 4 - This objective was completed entirely independently by the author, with all procedures, analyses, and interpretations conducted without involvement from other research teams. The findings represent the author's original work.

Chapter 2 Descriptive analysis of information on feral pigs in Scotland

Introduction

The presence of feral pigs has been documented in several regions of Scotland, and their numbers may increase significantly (Massei & Ward, 2022). The rooting and foraging behaviour of these species has been demonstrated to cause considerable agricultural and ecological damage, including crop losses, soil disturbance, and impacts on native vegetation (NatureScot, 2022). More importantly, feral pigs may act as a reservoir or bridge host for serious livestock diseases. In recent years, ASF has spread extensively across Europe, highlighting the potential risk that feral pig populations could pose to the United Kingdom if the virus were to be introduced (Cukor et al., 2020; EFSA, 2018b). Despite these concerns, however, knowledge about feral pigs in Scotland remains fragmentary. To date, no systematic survey of their abundance or distribution has been undertaken, and most estimates rely on localised observations or anecdotal reports (NatureScot, 2022). Furthermore, data concerning population dynamics, habitat use, and interactions with domestic livestock is scarce. These gaps in understanding have been shown to engender substantial uncertainty in ASF risk assessments and to hinder the development of effective contingency planning (EFSA, 2021).

The aim of this chapter is therefore to provide a descriptive analysis of the available information on feral pigs in Scotland. By collating and summarising existing reports, this chapter seeks to establish a foundational understanding of the current status and to identify the key knowledge gaps that must be addressed in order to support effective disease preparedness and management.

Methods

Data exploration

All available data sets on feral pigs in Scotland were sought using multiple approaches. Relevant unpublished sources, including Dell, (2020, thesis), and Adair (2015, thesis), as

well as the published study by Lovell et al. (2024), were reviewed, and grey literature was also examined. No other relevant published studies were identified. In addition, discussions were held with NatureScot about camera trap survey data in Scotland.
UK feral pig (*Sus scrofa*) sightings registered and published on the National Biodiversity Network (NBN) website by the end of April 2025 were included in the analysis. Raw data were downloaded in CSV file format from the NBN website. Of all the data, only those for which the province of sighting was Scotland were extracted, saved as a CSV file, and used for mapping and analysis.

Mapping of the data

QGIS (QGIS.org, 2023) was used to plot the sightings data and produce sightings heat maps. The open-source standard world map (GSI, 2023) and the Scotland Country Boundary map (Blackwood, 2017) were used for the base maps.

Analysis

R and its packages dplyr, ggplot2, and ggbreak were used to organise and visualise the data for descriptive analysis (R Core Team, 2021; Wickham, 2016; Wickham et al., 2023; Xu et al., 2021). For further information on the source of the sightings, the 'Data Partners' section of the NBN Atlas was consulted (NBN Trust, 2023). The datasets underpinning the data source were tabulated, and their reliability was evaluated on a three-level scale (high, medium, low). The evaluation considered data consistency (whether compiled from multiple sources with differing standards or from a unified standard), the accuracy of geographical information and reporting dates, and the condition of animals (sightings of live individuals, hunted specimens, or carcasses).

Results

Available data

Ultimately, the only data available for further consideration from published or publicly accessible sources was the data held in the NBN database. Information on the presence and distribution of feral pigs in Scotland was very limited as there is no national monitoring system for feral pigs. Efforts were made to collect all information on feral pig sightings and culls on the National Biodiversity Network (NBN) (website: https://species.nbnatlas.org/species/NBNSYS0000005142#tab_recordsView). Hunting of feral pigs is permitted in Scotland, but only landowner permission is required to shoot feral pigs on private land and no records of hunting activity are collected unless they are submitted to NBN.

Lovell et al. (2024) analysed the ecological characteristics of feral pigs in the Inverness region of Scotland (Bunloit Estate, Inverness-shire) using camera trap survey data collected between 2014 and 2015. The results showed that feral pigs preferred land cover types such as grassland and woodland, and tended to avoid areas such as coniferous plantations and heathland. Furthermore, their appearance frequency exhibited temporal and seasonal variations, with particularly pronounced nocturnal activity. The study also reported that human disturbance, as assessed by proximity to settlements and buildings and distance from roads and tracks, did not significantly impact their distribution.

Relevant unpublished studies were also considered. A study by Dell (2020) on the impact of feral pigs in Scotland revealed that the main concern amongst stakeholders was the potential impact on the spread of diseases such as ASF. His modelling of the feral pig population dynamics in Dumfries and Galloway, based on NBN records, predicted an increase in the population over the next decade and raised concerns about the worsening impact of feral pigs on livestock farms in the New Abbey area (Dell, 2020). Meanwhile, it was noted as a limitation that the predicted population might not represent the current situation, as the locations of the sightings were not in the best foraging and breeding habitats and were likely to be individuals passing through rather than residents (Dell, 2020).

There are camera trap surveys conducted by NatureScot in 2015 and 2016, but these data have not been made publicly available, although some may be included in the NBN data.

Overview of the NBN data

A total of 900 sightings were recorded, of which 513 were in Scotland, 337 in England, 12 in Wales, 1 in Northern Ireland, and 37 where the county of sighting was not specified. The data for Scotland consisted of data from multiple data providers and datasets, with 11 datasets provided by seven data providers.

Sources of sightings

As the data source is comprised of several datasets, it is essential to identify differences in each of their reporting criteria to understand potential biases in the data. NatureScot was the main data provider for Scotland, with 442 records. This was followed by the Mammal Society, the Highland Biological Recording Group, and the North East Scotland Biological Records Centre, with 38, 14, and 10 records, respectively. By dataset, wild boar sightings recorded by one individual (AR) and wild boar culled on the National Forest Estate Scotland 2015-21 accounted for the majority of data, with 205 and 100, respectively. Details of the data criteria for main datasets are summarised in table 1.

Table 1. Sources of the NBN data organised by data set.
A table summarising data details for the six main datasets comprising the NBN data, including reported animal status, reporting period and number of reports. The confidence level of the data, which was qualitatively estimated based on the reporting criteria of the data, was also included.

Data provider	Dataset Name	Data Source	Status of animals recorded	Place / grid references	Time recorded	Number of reports	Degree of confidence	Citation
NatureScot	Wild boar sightings held by Andy Riches (AR)	Multiple sourced data. The majority have been verified by Andy Riches, but a few could not be due to either the anonymous nature of the recorder or the time lapse since sighting. The original data were held by Andy Riches, Mammal Recorder for Dumfries & Galloway.	Sightings, field signs, game bags	Note: for some data, only approximate OS grid references are (estates where boar are hunted for sport did not wish to be identified)	from 2011	205	○ Medium	NatureScot (2025a)
NatureScot	Wild boar culled on the National Forest Estate Scotland 2015-21	Records of feral pigs culled on Forest Enterprise Scotland (FES) land. The original data were held by Forestry Commission Scotland (FCS)	Culled (shot by experienced FES staff or their agents)	Forest Enterprise Scotland (FES) land	during 2015-21	100	◎ High	NatureScot (2025b)
NatureScot	Feral Pigs - Sightings and Cull records - 2014-21	Records of feral pigs reported by landowners and occupiers in Scotland.	mainly culled, some are sighted	Hectad (10x10 km square) containing the centroid of that locality.	during 2014-21 Note: the date was all recorded as 1st July.	71	○ Medium	NatureScot (2025c)

Data provider	Dataset Name	Data Source	Status of animals recorded	Place / grid references	Time recorded	Number of reports	Degree of confidence	Citation
NatureScot	Wild boar SASA sightings record	Multiple sourced data. Note: some reports were harvested from extensive Google searches of news sites and forums. The original data were held by Science and Advice for Scottish Agriculture (SASA), a Division of the Scottish Government Agriculture, Food and Rural Communities Directorate.	Not specified	Inferred in most cases and should be assumed to be accurate to 1 km at best.	from 1976 to 2015 Note: Many dates are only approximate. Only the year was recorded for dates in most (41) records.	46	△ Low	NatureScot (2025d)
Mammal Society	National Mammal Atlas Project, online recording	Sightings were gathered via an online recording form, that were then validated based on recorder credentials and expert review by mammal experts. Many records also have a photograph attached to aid verification.	Not specified	Majority of data are provided with 100m or greater precision.	from 2012 to 2022	38	○ Medium	Mammal Society (2025)
NatureScot	Lochaber wild boar/feral pig camera trap survey, 2015	Camera trap data for a pilot survey of wild boar/feral pig aiming to understand the usage of different habitat types.	Live (recorded by camera-traps)	The National Forest Estate in the Glen Garry area of Lochaber, Inverness-shire	All records were dated in July 2014 or 2015, except one (June 2015).	20	○ Medium	NA

Location of sightings in Scotland

Sightings were plotted, coloured by dataset, to show the geographical distribution of sightings and datasets (Figure 2). The highest densities of points occur in the Great Glen and Dumfries and Galloway areas. Some datasets cover only parts of the country, which may introduce bias in the observed reporting patterns.

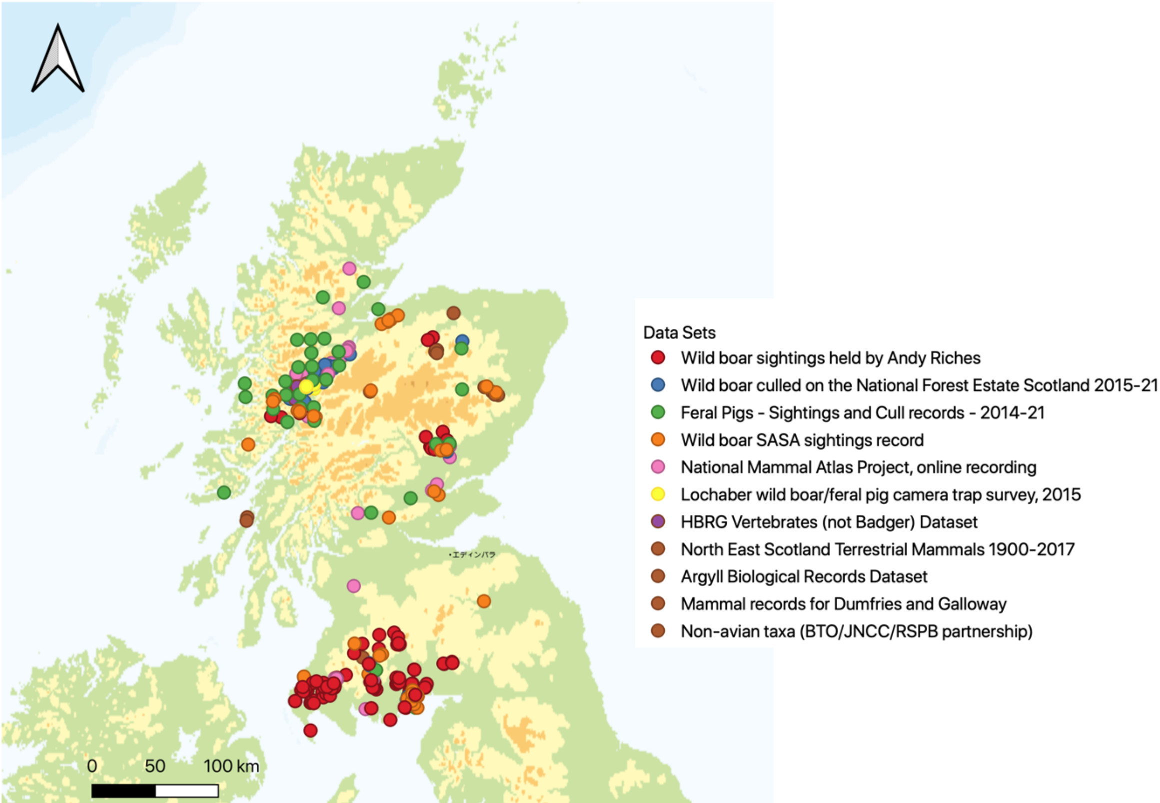

Figure 2. Locations of feral pig sightings in Scotland derived from the full set of available records used in this study (data up to April 2025), including those from the six main datasets summarised in Table 1.

As Figure 2 shows that many of the plots overlap in the given areas, a heat map of the number of feral pig sightings was created using the same data to visualise the concentration of sightings (Figure 3). The heatmap indicated a high concentration of sightings in part of Dumfries and Galloway. The second highest sightings were reported in Great Glen, and there appeared to be scattered sightings in east central Scotland.

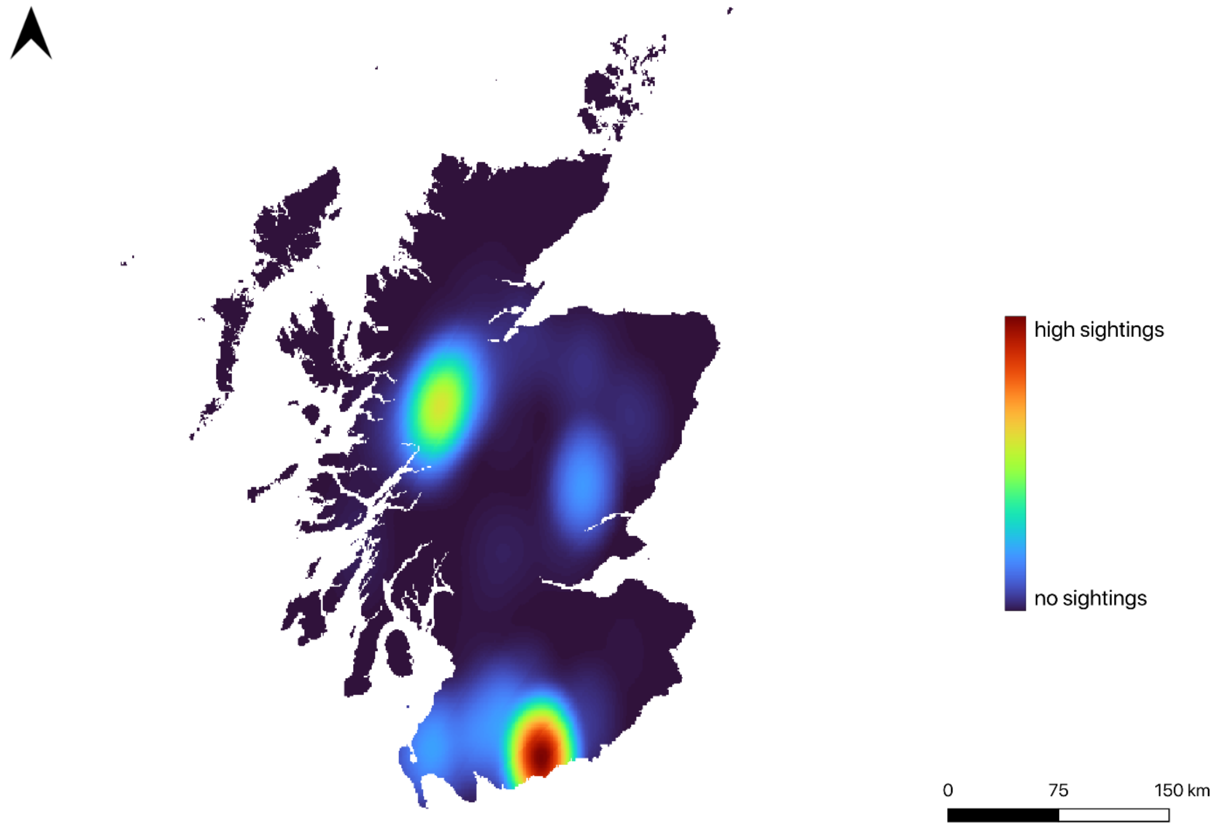

Figure 3. Heatmap (0.5 km radius) showing the locations of feral pig sightings in Scotland.

Areas with no sightings are shown in dark blue, with higher numbers of sightings shown in red.

Changes in the number of sightings over time

The annual count of sightings showed that recent sightings began to be reported in 2002, with an increase from 2010 and a peak in 2014, followed by less than 10 reported sightings from 2020.

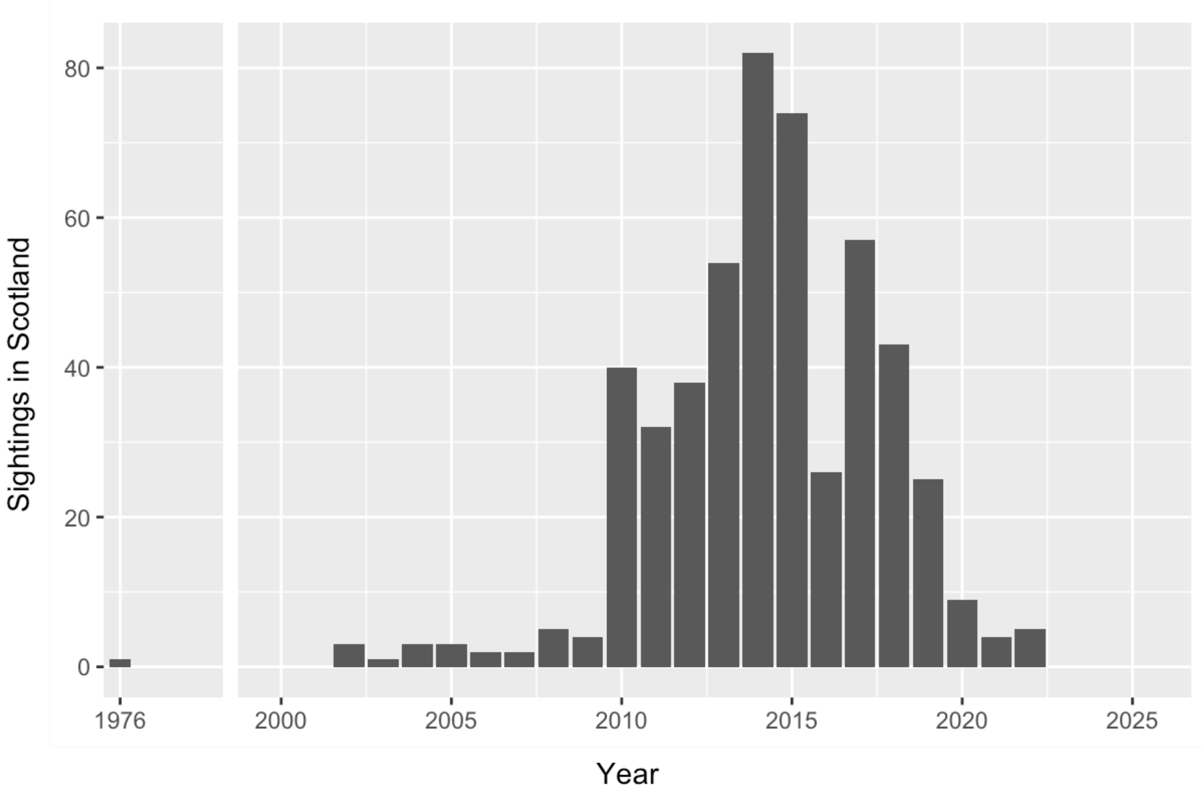

Figure 4. Number of feral pig sightings in Scotland per year (annual counts, not cumulative).
The figure shows temporal variation in reported sightings, illustrating changes in reporting frequency over time.

In order to explore the spatial distribution over time, sightings were plotted on the maps for 1976, the first year of sightings reported; 2002, the first sighting in recent years; 2010, when the number of sightings increased, and the year before; and every five years thereafter, in 2015 (just after the peak) and 2020 (Figure 4).

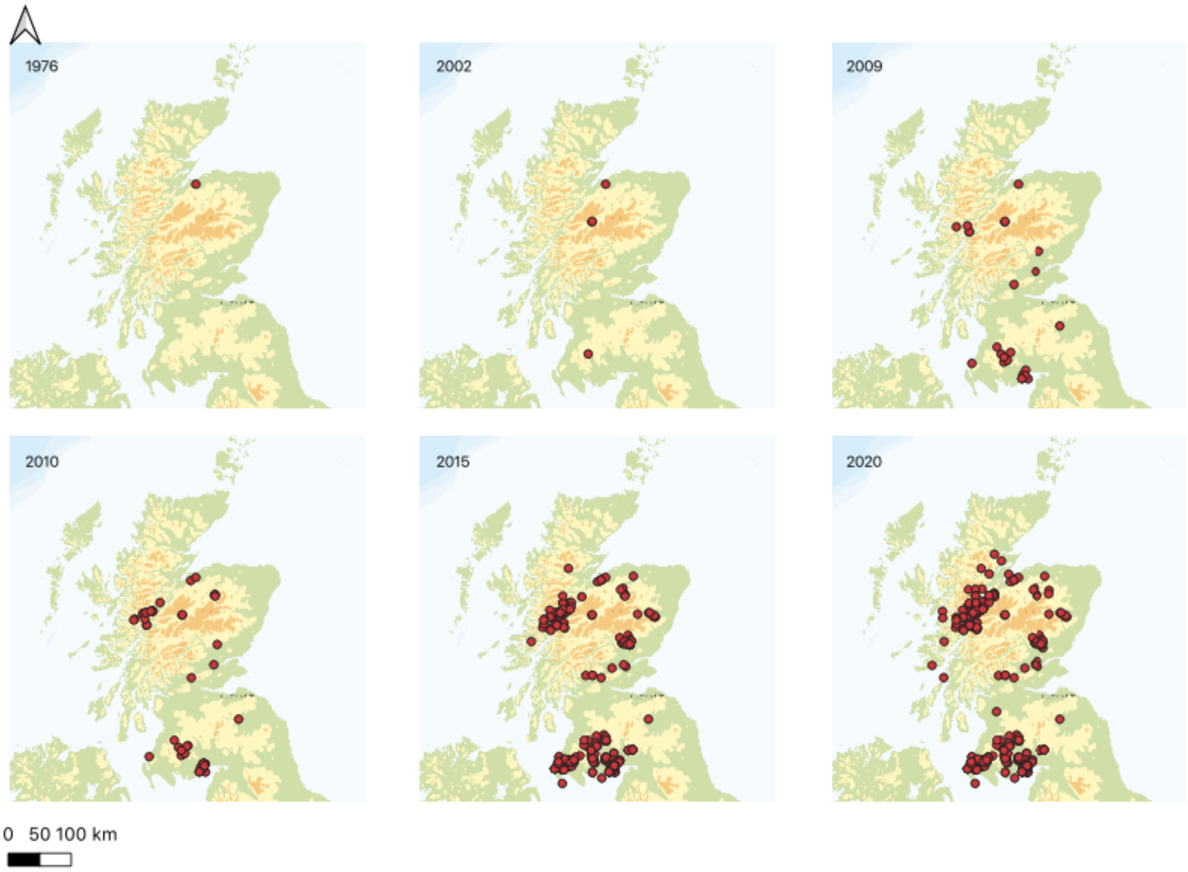

Figure 5. Locations of feral pig sightings in 1976, 2002, 2009, 2010, 2015 and 2020 (from top left to bottom right).

Red dots represent the cumulative locations of reported feral pig sightings up to each respective year (i.e. including all sightings recorded up to that year). The scale is 1:3,500,000.

The chronological distribution of sighting sites (Figure 5) reveals that, overall, sightings of feral pigs have increased in Great Glen and Dumfries and Galloway contemporaneously. Feral pigs were first sighted in Great Glen in 1976, and the first sightings of the recent increase were in both Great Glen and Dumfries and Galloway in 2002. By 2009, there had been an increase in sightings in both areas, and reports of sightings in east central Scotland. Figure 4 shows that sightings began to increase from 2010. However, comparison with the spatial distribution in 2009 (Figure 5) indicates that this increase occurred primarily in the Great Glen area, rather than being widespread across Scotland. Subsequently, there was a significant increase in the number and distribution of sightings in the Great Glen, Dumfries and Galloway and the east central region by 2015. By 2020, sightings had spread further north and west, reaching around Dornoch Bay in the north and the Isle of Mull in the west.

Seasonal changes in the number of sightings

Monthly counts of sightings (Figure 6), excluding 53 cases with no information on the month of sighting, show that the highest number is in July, accounting for almost one-fifth of all sightings. However, as shown in the summary table of datasets (Table 1), one dataset, where all sightings were recorded as 1 July, contributed to the high number of sightings in July. The next most frequent months are May, April, and March, in that order, with a range of 53-73 sightings. This is followed by October, with 41 sightings. Winter (November-February) has fewer sightings, with less than 16, and January has the lowest with 12 sightings.

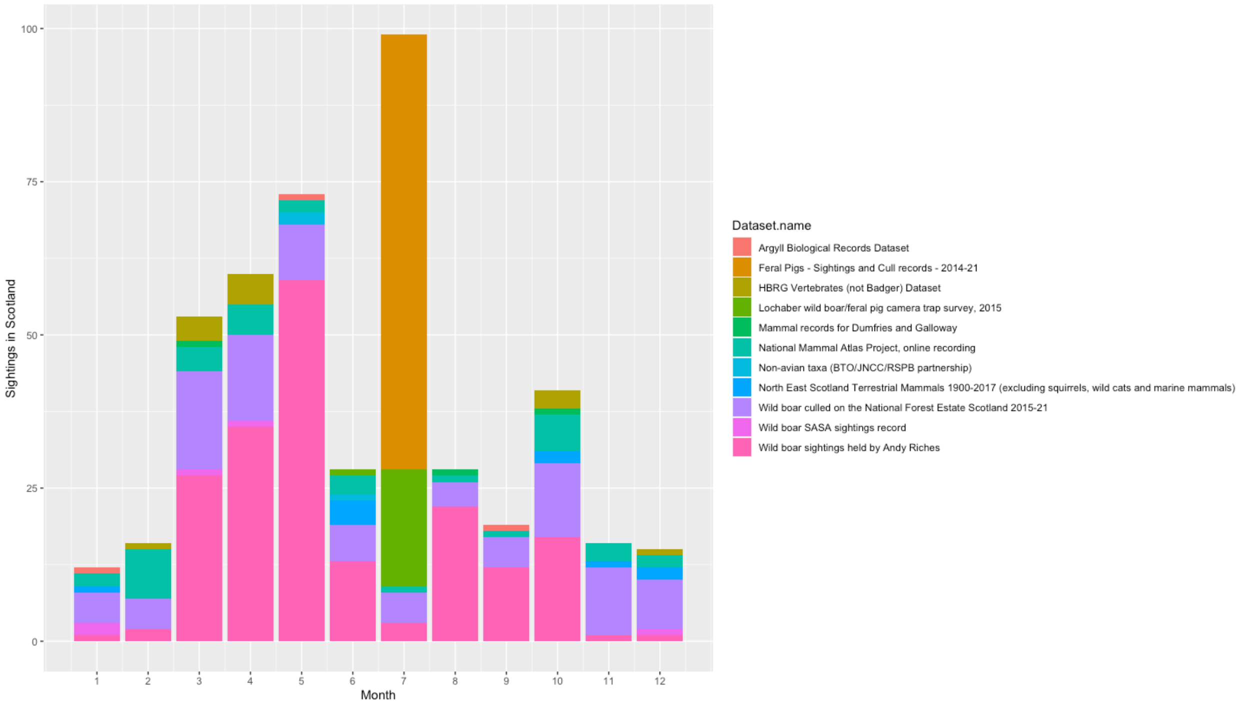

Figure 6. Number of sightings per month coloured by dataset.
Bars represent the total number of sightings per year, with colours indicating contributions from different datasets. Note that in total, there are 53 datapoints with missing month information: 41 from the Wild boar SASA sightings record and 12 from Wild boar sightings held by AR.

Looking at seasonal changes by year (Figure 7), apart from the obvious July spike for the reason mentioned above, there were changes in the main dataset: from 2010 to 2015, Wild boar sightings recorded by AR (pink bars in Figure 7), and from 2016 onwards, Wild boar culled on the National Forest Estate Scotland 2015-21 (purple bar) was the main dataset from which the sightings came.

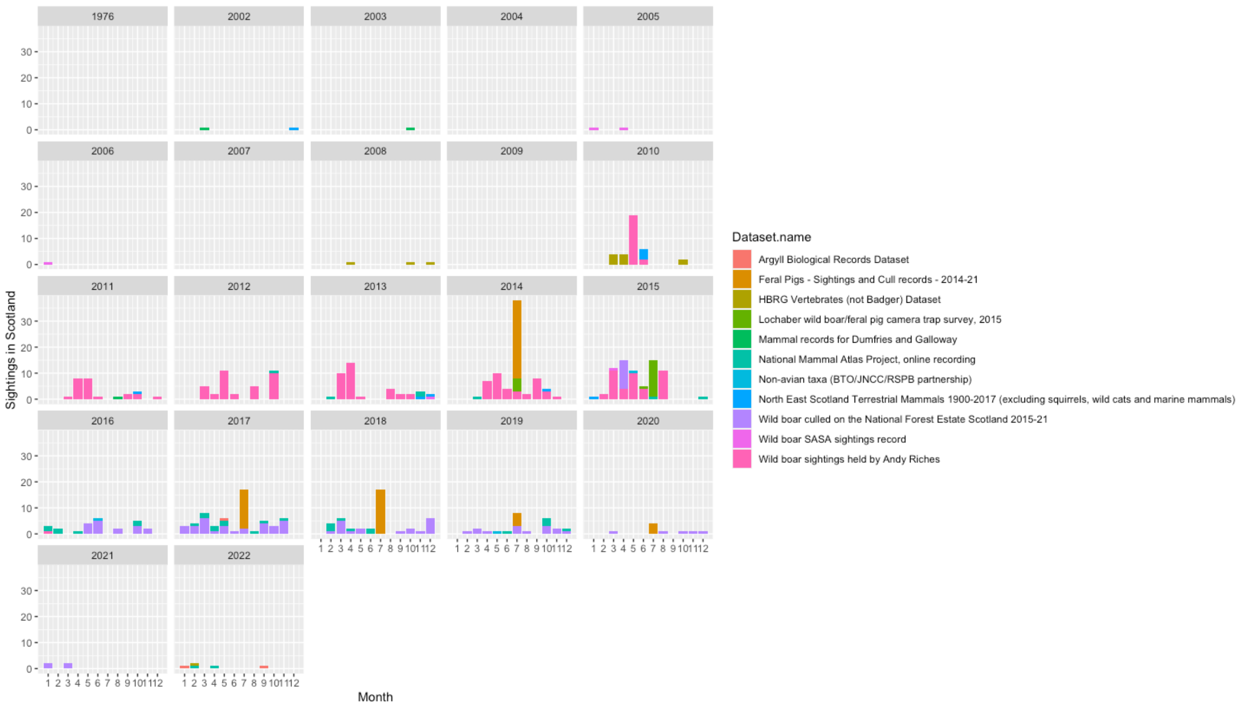

Figure 7. Number of monthly sightings per year coloured by dataset.

Each panel represents a different year, showing the distribution of sightings across months and highlighting variation in reporting patterns between datasets over time.

Discussion

With ASF becoming a global threat, the importance of the role of wild boar and their carcasses in disease dynamics has been recognised in Europe, highlighting the importance of wild boar management (Johann et al., 2020; Sauter-Louis et al., 2021). In Scotland, where ASF has not been introduced, systematic information on the abundance and distribution of feral pigs provides important information for ASF prevention and control measures.

In exploring the available data on the abundance of feral pigs in Scotland, the only data available for this study was the NBN Atlas, where efforts have been made to compile information on feral pigs in Scotland. Sightings were concentrated in the Dumfries and Galloway area and Great Glen. As the data consists of several datasets with different reporting criteria and many are voluntary reports of sightings, it is considered that caution is warranted in processing and interpreting the data and that more accurate and systematic data is needed to estimate the exact population status or to infer any specific trends in feral pigs.

In general, the sighting and hunting data could conceivably be influenced by : (1) reporting/hunting effort (Keuling et al., 2018), (2) food availability (negatively correlated with the extent of feral pig activity) (Keuling et al., 2009; Singer et al., 1981), and (3) the area of human activity (i.e. sightings cannot be reported outside the area of human activity, even if feral pigs are present in the area. It is also possible that fewer people visited feral pig habitat for recreation during the COVID-19 lockdown). There are also limitations due to the animal's nocturnal habits (Keuling et al., 2018). It would therefore be difficult to describe trends in abundance and distribution over time without consistent data from well-planned surveys carried out over time.

Although the NBN is a valuable resource in collating feral pig sightings, it is very important to note that the data is made up of multiple datasets from several providers, as they all differ in terms of time period covered, reporting criteria, status of feral pigs (i.e., culled, alive or just signs) and the extent to which location information is accurate. This manifests in several potential sources of bias. It should also be noted that these data are "presence-only" records, meaning that information is only available where feral pigs were observed, with no explicit data on where they were absent. Presence-only data are subject to several potential sources of bias (Pearce & Boyce, 2005). For example, sightings are likely to be concentrated in areas that are easily accessible to observers or frequently visited by people, leading to a geographic bias. Temporal bias may occur if observations are recorded predominantly during certain seasons or years. Observer behaviour and interest can also influence reporting, with more conspicuous or charismatic animals being preferentially reported. Additionally, different datasets may have varying criteria for what constitutes a sighting and differing accuracy in location information. While statistical methods exist to exploit presence-only data, these biases make reliable inference about distribution and abundance particularly challenging. For example, when looking at seasonality, there were more sightings in July than in other months. However, this could be an artifact because (1) all sightings in the dataset "Feral Pigs - Sightings and Cull records - 2014-21", which accounted for the majority of total sightings, were dated 1 July, and (2) all data from "Lochaber wild boar/feral pig camera trap survey, 2015" were recorded in July. This camera trap survey was recorded only in 2014 and 2015, contributing to the large number of sightings in these years. Based on the above, it was considered difficult to attempt to derive specific trends from the data, given that it consists of a variety of sources, including short-term observational survey results.

Effective management of feral pigs for disease prevention and control, including ASF, requires knowledge of their distribution and density (Keuling et al., 2018). However, as far as has been explored, the information currently available on feral pigs in Scotland would not be reliable enough to provide population estimates. Furthermore, the absence of any new Scotland-wide data over the past two years is a matter of considerable concern. Given that the existing datasets remain the only comprehensive sources available, this highlights the ongoing challenges in collecting and integrating national-level data. Addressing these challenges is therefore essential for building more reliable and systematic information on the abundance and distribution of feral pigs in Scotland.

Systematic data of sufficient quantity and more standardised and consistent records would be needed to measure the range, status, and density of feral pigs with some degree of confidence. ESFA recommended the following methods for estimating wild boar populations and densities: camera trapping, drive counts and thermographic distance sampling, for estimating wild boar densities at a regional scale (Keuling et al., 2018). Hunting data with detailed spatial scales are also considered most likely to be used to describe long-term trends at larger spatial scales (Keuling et al., 2018). Feral pig populations in the Forest of Dean, England, have been monitored annually since 2013 using a distance sampling/thermal imaging technique developed by Forest Research, which has been shown to be effective in estimating wild ungulate populations in forested areas with limited visibility (Forestry England, 2022; Gill, 2022b). In Scotland, Adair (2015) and NatureScot (see Table 1) have conducted a pilot study using camera traps to monitor feral pig population in a regional area, which will hopefully lead to further development of feral pig population surveys in the future.

The management of feral pigs is a challenge not only in terms of disease control, including ASF, but also in terms of various aspects such as damage to crops and livestock, ecological impacts, and traffic hazards (Palencia et al., 2023). Building reliable and systematic data on the abundance and distribution of feral pigs in Scotland would be essential not only for ASF contingency planning but also in many other areas, and represents an urgent priority that requires immediate attention.

Chapter 3 Feral – domestic pig interactions in outdoor pig farmers in Scotland

Introduction

In the previous chapter, I analysed the available data on feral pigs in Scotland, identified key knowledge gaps, and highlighted the need for more comprehensive information. A previous survey in Scotland revealed that approximately one-third of pig holdings are located within 20 km of feral pig sightings, most of which are smallholders (Porphyre et al., 2020). EFSA has recognised outdoor pig farms as being at a substantial risk of ASF introduction and spread, particularly when outdoor areas are adjacent to forests or regions inhabited by wild boar, where direct or indirect contact is possible. There has also been a report from Scotland of feral pigs entering a pig shed (Dell, 2020). However, to the best of my knowledge, no studies have been conducted in Scotland to investigate interactions between feral pigs and domestic pigs, nor is there any quantitative data available on such interactions.

Direct observation of interactions between feral pigs and domestic pigs is logistically challenging and resource-intensive, particularly across wide geographic areas. Farmer-based surveys provide a practical alternative, enabling the collection of local knowledge and first-hand reports of sightings, incursions, or evidence of contact that would otherwise remain undocumented (Brook & McLachlan, 2006). Such approaches have been widely used to characterize wild boar interactions with agriculture, for example in studies of crop damage and livestock exposure (Schley et al., 2008). Moreover, risk assessments for transboundary animal diseases, including African swine fever, have relied on survey data to evaluate the likelihood of direct or indirect contacts between wild boar and domestic pig holdings (Barasona et al., 2014; EFSA, 2018b). For these reasons, farmer surveys represent an appropriate and established method to capture information on potential interactions between feral pigs and domestic pigs in Scotland.

Therefore, in this chapter, we conducted a questionnaire survey on interactions between feral pigs and domestic pigs in Scotland, with the aim of gaining insight into their occurrence and attempting to quantify such interactions. Specifically, the objectives were to measure the rate of contact between feral and domestic pigs, describe the types of interactions observed, and estimate the group sizes of feral pigs reported.

Methods

Questionnaire survey

The questions on interactions between feral pigs and domestic pigs were included as part of a wider questionnaire to pig keepers in Scotland. Since the questionnaire was therefore undertaken jointly with another student, I first summarise the overall methodology for completeness, and subsequently focus on the analysis of the questions I led, relating to interactions between feral and domestic pigs.

Target population and sample size

This study was aimed at owners or managers of pig farms where pigs are kept outdoors or have access to the outdoors in areas where feral pigs are thought to be present. As a list of registered pig producers in Scotland is unavailable due to the UK's GDPR legislation, the survey was advertised via a dissemination flyer containing a survey link and QR code. The flyer was shared on social media platforms (Facebook, Twitter, LinkedIn) and on online smallholder forums, including Scottish Smallholder groups, breed groups such as Oxford Sandy and Black pigs, Large Black pigs and Kune Kune pigs sites. We also requested the National Farmers Union of Scotland, Quality Meat Scotland, and British Pig Association to circulate the survey link to their pig group members.

Sample size calculation

Assuming 50% response to a binary question (e.g. have you seen any activity signs of feral pigs/wild boar around your farm), with a desired confidence level of 95% and an error of ±10.0%, the sample size was calculated to be 95.

Online questionnaire survey

The questionnaire for this survey was generated using university approved Qualtrics XM software (Qualtrics, 2023) and circulated online, with advice provided by the Scottish

Government Centre of Expertise on Animal Disease Outbreaks (EPIC), regarding its content. Respondents were able to complete the questionnaire during the period from 1 August to 30 November 2023. Questions on the potential for contact between domestic pigs and feral pigs were included in a questionnaire developed by another PhD student designed to describe the management and biosecurity practices on outdoor pig farms in Scotland. Most questions are closed-ended questions, that simply require the participant to choose an answer from a list of options. The questions related to potential contact and frequency of contact are listed in the table (Table 2). Respondents were not asked to recall observations over a specified time period, and responses may therefore reflect varying recall windows depending on individual interpretation.

Table 2. List of the questions related to feral – domestic pig interactions.

Question
1. Have you seen any activity signs of feral pigs/wild boar around your farm? (e.g., rubbing, tracks or trails, feral pigs/wild boar nest, damage to fence or feed or crops)
2. How often do you see these signs?
3. Have you seen feral pigs/wild boar visiting your pig farm? (Visiting: feral pigs/wild boar within the perimeter of the farm or just outside)
4. How often do you see feral pigs/wild boar visiting your farm?
5. How many feral pigs/wild boar do you usually see at one time?
6. Which of following describe the situation when you see feral pigs/wild boar on your farm? (as many as apply)
7. How often do you see feral pig/wild boar having direct physical contact with your pigs?

Ethics

The survey was conducted with the approval of the MVLS College Ethics Committee of the University of Glasgow (approval No. 200220178). All data collected was anonymous, with no personal data and no sensitive personal data/special categories of data. Prior to the conduct of the survey, informed consent was obtained from all participants. Participants were informed that the survey was voluntary, that it was confidential, and that they could withdraw from participation at any time.

Quantifying the contact frequency

Different ordinal qualitative forms; none / at least once a year / at least once a month / at least once a week / at least once a day for the frequency of visits of feral pigs in the vicinity of the farm and contacts with domestic pigs were transformed into ordinal values; 0 / 1 / 12 / 52 / 365, corresponding to the estimated annual number of visits/contacts (Payne et al., 2018). No responses were obtained to the question regarding direct contact between feral and domestic pigs; instead, contact was inferred by aggregating participants who selected "physical contact" as a reason for visits. The denominators for calculating the frequencies of sightings, visits, and contacts included all respondents who answered the respective questions.

Results

Survey response

A total of 35 questionnaires were returned. Of these, seven were excluded from the dataset: three were discontinued immediately after consent, and four did not satisfy the inclusion requirement of keeping at least one pig outdoors. Accordingly, 28 questionnaires were retained for analysis. Of the retained questionnaires, responses were geographically distributed across Scotland, with postcode districts AB, DG, EH, G, IV, ML, and TD represented.

Frequency of contact calculation

A total of 24 people involved in outdoor pig farming in Scotland responded to the survey question about feral pigs. Of these, four (16.7%) had seen signs of feral pigs on their farm at least once a month. Three respondents (12.5%) had witnessed a visit, two of them at least once a month and one at least once a year (Table 3). In terms of the nature of these visits, each respondent reported observing 7 to 10 feral pigs during a single visit. The specific encounters included piglets being contacted, fighting with adult pigs, and the presence of a feral pig just outside the farm perimeter. Two (8.3%) respondents observed physical contact between feral pigs and their domestic pigs, one at least once a month and the other once a year. Based on the observed events and their frequencies, the annual incidence probabilities per farm were calculated to be 2 signs (0.0055 signs/farm/day), 0.58 visits (0.0016 visits/farm/day), and 0.54 contacts (0.0015 contacts/farm/day).

Table 3. The number of responses for each observed event and the calculated frequency.

		Respondents (n=24)
Sign	Observed	4 (16.7%)
	Observed once a year	0
	Observed once a month	4
	Annual frequency	2.0
	Daily frequency	0.005479452
	Probability of contact	0.5 (2/4)
Visit	Observed	3 (12.5%)
	Observed once a year	2
	Observed once a month	1
	Annual frequency	0.5833333
	Daily frequency	0.001598174
	Probability of contact	0.67 (2/3)
Contact	Observed	2 (8.3%)
	Observed once a year	1
	Observed once a month	1
	Annual frequency	0.5416667
	Daily frequency	0.001484018

Discussion

Wild boar are recognised as a major risk factor for outdoor pig farms, as they are potential mediators of ASF transmission. In its Scientific Opinion, the European Food Safety Authority (EFSA) evaluated the risk of ASF being introduced to outdoor pig farms via wild boar as high (EFSA, 2021). In Scotland, where large numbers of smallholders keep pigs outdoors (Porphyre et al., 2014), the presence of feral pigs could pose a significant threat to the introduction of ASF and other notifiable livestock diseases. However, data on farm visits and direct or indirect contact between feral and domestic pigs is very limited and has not yet been quantified. This chapter therefore attempts to provide, for the first time in Scotland, reports and preliminary estimates of potential interactions between feral and outdoor-reared domestic pigs, based on a survey.

As a result, although only a minority of respondents reported signs of feral pigs on or around their farms, the calculated annual frequencies of signs, visits, and direct contacts indicate that such interactions do occur and may not be negligible. In particular, the reports of direct contact, albeit infrequent, highlight the potential for disease transmission between feral and domestic populations. These findings suggest that outdoor pig farms in areas where feral pigs are present could face a measurable risk of pathogen introduction, even if the observed contact rates appear relatively low.

Regarding the denominators used to calculate the frequencies of sightings, visits, and contacts, an initial attempt was made to restrict them to respondents located in postcode districts with feral pig reports in the NBN database. However, because only the first three digits of the postcode were available, respondents could not be accurately narrowed down. Notably, three of the four participants who reported sightings, visits, or contacts were from districts without NBN records, suggesting that feral pigs may be more widespread than indicated by the database. This finding highlights the possibility that official records alone may underestimate the presence of feral pigs. Nevertheless, it cannot be ruled out that some respondents reported their home postcode rather than that of their farm, which may also contribute to these discrepancies.

The interactions reported in our survey included contact with piglets, aggressive encounters with domestic pigs, and the presence of feral pigs just outside farm boundaries. This differs from the description in Dell (2020), a survey conducted in Scotland, where the only previous report involved a feral pig repeatedly entering a farm to mate with sows. In Scotland, more than half of breeding sows are kept in outdoor breeding systems (Scottish Government, 2021), which inherently increases the likelihood of wildlife–livestock contact. Our survey, however, revealed a broader spectrum of interactions, suggesting that visits by feral pigs may occur for reasons beyond reproduction, including foraging or access to water. Interestingly, respondents reported that multiple feral pigs (7–10 individuals) visited farms simultaneously, indicating that visits were not limited to dispersed males but may involve small groups, reflecting social or herd-based behaviours. Such collective visits could increase the potential for direct and indirect pathogen transmission compared to solitary individuals. Although mating events were not captured in our survey, exploratory or aggressive interactions were observed, highlighting that even non-reproductive visits can pose measurable risks for outdoor pig farms. Importantly, EFSA (2021) highlights that shared resources such as water and feed represent significant pathways for indirect contact and pathogen transmission, reinforcing that these diverse types of interactions should be considered in risk assessments.

While these findings provide preliminary insights into feral pig visits and interactions with outdoor domestic pigs in Scotland, several limitations should be considered. First, the survey may not be representative of all outdoor pig farms in Scotland, as participation was voluntary and limited to 24 respondents. This could introduce a self-selection bias: farmers who are particularly interested in feral pigs or who have observed them on their farms may have been more likely to participate, potentially leading to overestimation of feral pig visits and interactions. Observation bias is also likely, particularly given the nocturnal activity patterns of feral pigs (Lovell et al., 2024), which may have led to underreporting. Additionally, the farms surveyed differ in their surrounding feral pig density and proximity to feral pig habitats, which may influence the likelihood of visits and contacts. Finally, as no specific recall period was defined in the questionnaire, responses may reflect different time frames depending on individual interpretation, potentially introducing additional variability and recall bias in the reported observations.

Consequently, the annual incidence probabilities calculated from observed events should be interpreted with caution and should not be directly used as inputs for epidemiological models without further validation. These limitations highlight the need for additional, systematic studies to better quantify the frequency and drivers of feral pig–domestic pig interactions across Scotland. For example, GPS tracking, camera trapping, or systematic field observations could be used to monitor feral pig movements and interactions with domestic pigs across different regions and seasons.

Chapter 4 Modelling of ASF in feral pigs

Introduction

As demonstrated in previous chapters, feral pig populations have been reported in Scotland, with contact between feral and domestic pigs also observed. The introduction of ASFV to these populations could pose a serious threat to the pig farming industry and the broader ecosystem (Dixon et al., 2020). Accordingly, risk management measures targeting feral pigs are a potential route of control (Morelle et al., 2020). However, owing to the scarcity of reliable ecological data on feral pigs in Scotland, to the best of my knowledge, no studies have so far investigated the potential dynamics of ASF following its introduction into these populations.

Survey results in the previous chapter indicated that the observed frequencies of feral pig signs, visits, and contacts were very low, with annual probabilities of 0.0055, 0.0016, and 0.0015 events per farm per day, respectively. However, because these figures rely solely on farmers' visual detection, they are likely to underestimate the true frequency of interactions. To better understand how interactions between feral and domestic pigs might impact ASF transmission, empirical observations can be explored in a modelling framework.

To place the present modelling approach in context, it is important to consider existing modelling frameworks for ASF in wild boar populations. A range of modelling approaches has been developed to investigate ASF dynamics in wild boar populations, many of which are spatially explicit and individual-based, and build on the framework established by Lange and Thulke (2017), with subsequent adaptations by Halasa et al. (2019) and Salazar et al. (2022). These models have provided important insights into transmission dynamics and persistence under different ecological conditions. However, their direct applicability to Scotland is limited due to differences in data availability, population structure, and landscape characteristics. Although a density of 1 head/km² was considered a plausible baseline scenario for Scotland, reflecting current understanding of feral pig populations, substantial uncertainty remains. The model developed in this study therefore builds on existing approaches by incorporating key epidemiological and demographic parameters from previous studies, while exploring a range of population density scenarios. This allows both a baseline assessment of infection dynamics under plausible conditions and a broader evaluation of how variation in population density may influence ASF spread and persistence in feral pig populations in Scotland.

In this chapter, we develop a spatially explicit, individual-based simulation model. Although data on feral pigs in Scotland remain limited, this model makes use of the available information to provide a preliminary estimate of ASF spread and persistence in feral pig populations, and the associated farm-level exposure risk for ASF risk management and contingency planning, while also highlighting the need for further field data collection. Specifically, this study aims to (1) assess the extent and persistence of ASF spread following introduction into feral pig populations, (2) explore the population densities under which sustained transmission is unlikely, (3) set in context the farm visit frequencies and associated observation probabilities calculated from the survey data in the previous chapter. Through this modelling work, a link is established between empirical observations and simulation-based outcomes, thereby enabling a more informed assessment of feral–domestic pig interactions and informing ASF risk management and contingency planning.

Methods

Model Overview

This model simulates the spread of African swine fever (ASF) in feral pig populations, using the example of Dumfries and Galloway, Scotland, to provide insights for contingency planning and outbreak management. It is a spatially explicit model in which the landscape is divided into grid cells, allowing infection to spread both between individuals and across neighbouring groups. Pig demography and family group structure are incorporated, as close contact within groups and dispersal of young males strongly influence transmission. The model represents key infection dynamics, including latent and infectious periods, ASF-related mortality, and carcass-mediated environmental persistence, and tracks outcomes at both the individual and group level. In doing so, it addresses policy-relevant questions such as the probability of outbreak persistence, the minimum pig density required for sustained transmission, the threshold conditions under which infections fade out, and the potential underestimation of visit rates in farm-based surveillance. While habitat heterogeneity and variation in the carrying capacity of cells are not captured, the model nonetheless provides a valuable framework for understanding ASF dynamics in feral pigs and informing early detection and targeted interventions.

Model structure

The model describes the transmission of ASF in an individual-based stochastic model, with reference to the model previously developed by Lange & Thulke (2017), Halasa et al. (2019), and Salazar et al. (2022).

This model consisted of two components: feral pig demography and ASF infection dynamics. The population dynamics were simulated as the life cycle of individual feral pigs living in a landscape the size of the Dumfries and Galloway area divided into grid cells of about 4 km^2. Each week, stochastically selected individuals disperse and/or die naturally. Feral pigs live alone or in groups of two to 30 individuals. We assume a group size of 10 and each grid cell contains at most one group. Each animal was characterised by demographic, geographic and epidemiological information, including individual ID, geographical location (cell ID, x-y-axis), age (weeks), sex (male or female), life stage (infant, adult, or juvenile), and disease status (susceptible, exposed, infectious, recovered, or carcass).

Infection dynamics were modelled via a Susceptible - Exposed - Infectious - Recovered/Removed (SEIR) model, considering two routes of infection: (1) direct contact with infected cohorts in the same group, i.e. in the same grid cell; (2) direct contact with infected carcasses in the same group or in neighbouring cells.

Parameterisation

The model has no external data inputs. Parameters used for demographic and ASF dynamics are listed in Table 4.

Table 4. The values of the parameters used in a stochastic simulation model for the transmission of ASF in feral pigs.

Parameter	Value	Source
Feral pigs ecology		
Initial age distribution (upper age bound from1 to 11 years)	0.38, 0.24, 0.15, 0.09, 0.06, 0.03, 0.02, 0.01, 0.01, 0.01, 0.00	Kramer-Schadt et al. (2009); Lange & Thulke (2017)
Maximum age (week)	572	Lange & Thulke (2017)
Life stage (week)	1 to 3 (Infant), 4 to 12 (Juvenile), 13 and above (adult)	Croft et al. (2019)
Sex ratio	0.5	Croft et al. (2019)
Survival probability (weekly)	0.976 (Infant), 0.978 (Juvenile), 0.992 (Adult)	Croft et al. (2019)
Dispersal probability of young juveniles	1	Lange & Thulke (2017)
Dispersal step (weekly)	12 cells (24 km)	Lange & Thulke (2017)
Maximum dispersal steps	24 cells (48 km)	Lange & Thulke (2017)
ASF epidemiology		
Infection probability by direct transmission within group (daily)	0.007	Salazar et al. (2022)
Infection probability via a carcass within group (daily)	0.03	Salazar et al. (2022)
Infection probability via a carcass in a neighbouring cell (daily)	0.03	Salazar et al. (2022)
Latent period (days)	5	Adapted from Salazar et al. (2022)
Infectious period (days)	5	Croft et al. (2020)
Carcass persistence (days)	56	Croft et al. (2020)
Mortality due to infection	0.95	Salazar et al. (2022)

Demographic parameters

Age distribution

For the initial age distribution, figures from a 100-year model run of wild boar demography by Kramer-Schadt et al. (2009) were adopted. This was also the approach used by Halasa et al. (2019), Lange & Thulke (2017, 2015), and Salazar et al. (2022). The maximum age was set at 11 years. As the age increases, the proportion of the total population becomes very small. This distribution is consistent with a report that most feral pigs typically do not live longer than 6-8 years in the wild, with a maximum life span estimated at 9-10 years (Extension Foundation, 2019).

Sex ratio

As the sex ratio of male to female wild boars is usually 1:1 (Extension Foundation, 2019), this ratio was used as in Croft et al. (2020).

Survival rates and life stages

In previous models, some models adapted annual survival rates and others adopted weekly survival rates. In this model, the demographics were taken from Croft et al. (2020), which uses weekly survival rates, as the demographics are updated weekly. Survival rates depend on life stages. Therefore, the life stage classification was also taken from Croft et al. (2020), with infant, juvenile and adult as 1 to 3 weeks, 4 to 12 weeks, and 13 weeks or more, respectively.

Probability of dispersal

Based on the observations that dispersal is mainly sex-dependent (Truvé & Lemel, 2003) and that the main dispersers are young males (Keuling et al., 2010), the dispersal probability of young males from Lange & Thulke (2017) was used instead of the habitat-density-dependent probability from Croft et al. (2020). Seasonality was not considered because previous ASF observations have shown that the seasonality of boar movements, including what we call dispersal in this study, is not a sufficient predictor of ASF spatiotemporal dynamics (Podgórski & Śmietanka, 2018).

Table 5 summarises the parameters governing dispersal of juvenile males in several major ASF modelling studies, including timing, conditions, probability, direction, movement range, and duration. Even for a single behavioural process such as dispersal, these parameters vary widely between models, reflecting differences in spatial resolution, ecological assumptions, and modelling decisions. This diversity highlights the inherent complexity in parameterising dispersal behaviour in wild boar populations and underscores the care required when interpreting simulation outcomes.

Table 5. Parameters for dispersal of juvenile male wild boars in previous ASF epidemiological modelling studies.

The table summarises differences in timing, conditions, dispersal probability, movement direction, range, and duration across studies, illustrating both the diversity of modelling approaches and the complexity involved in representing dispersal behaviour.

	Lange & Thulke (2017)	Halasa et al. (2019)	Salazar et al. (2022)	Croft et al. (2019)
When dispersal occur	Over the weeks 25 and 30 (mid-June to end of July).	Dispersal (group split) will be tested once a year for each group, between the weeks 25 and 30.		The probability of dispersal increases as the patch population reaches carrying capacity.
Conditions for dispersal	NA	A group has an adult male and has at least two sub-adult males to split from the group (Lange, 2015). The splitting males would form a new group and disperse to join a female group.		NA (Note: this applies to all animals, not only juvenile males.
Dispersal probability	100 % (all subadult males disperse over the period)	Uniform (min = 0.25, max = 0.75) (Truve et al., 2004)	50 % (Adapted from Halasa et al., 2019)	Density-dependent probability: Settling reduction at carrying capacity of 0.976 (Infant), 0.978 (Juvenile), and 0.992 (Adult).
The direction	Each step can be either oriented (probability: 0.5) or straight ahead. Oriented movement: move to a cell with the most habitat-friendly environment in neibouring cells. Otherwise, continue in the previous direction.	First, the direction in which they will move throughout the dispersal is randomly chosen. Sub-adult males will then move to one of the three randomly selected cells in that direction.		The destination is determined randomly from neighbouring patches, considering the length of the shared boundaries.
Movement range (daily or weekly)	8 cells (24 km)/week (cell: 3 × 3 km) (Truvé & Lemel 2003)	0 or 1 cell/day (cell: 2 × 2 km)	1 or 2 cells/day (cell: 3 × 3km)	6 (male), 4 (female) patches /week
Until when dispersal continue	The movement ends when they reach the maximum dispersal steps of 16 cells (48 km) (Truvé & Lemel 2003)	Until they meet a female group without male. If they do not find a suitable cell by the end of the year, they will die.	Until they meet a female group without male.	Until they are unable to move any further without returning to the same patch or run out of movement steps.

Spatial distribution

Feral pigs live alone or in groups of two to 30 individuals (Dell, 2020). The groups are stable over long periods (Podgórski, Lusseau, et al., 2014) and typically occupy a home range of an area of approximately 4-8 km^2 (Keuling et al., 2008; Podgórski, Scandura, et al., 2014). To reflect these ecological characteristics, the study area was represented as a 20 × 20 km^2 landscape (400 km^2 in total), divided into 2 × 2 km grid cells (4 km^2 each), resulting in 100 cells. Each cell could host at most one group, which was considered the group's core home cell. Given that habitat ranges may extend up to 8 km^2, groups in this model could overlap with neighbouring cells, and such spatial overlap creates opportunities for transmission between adjacent groups.

The spatial resolution and landscape structure adopted here were designed to reflect the ecological scale of wild boar home ranges, taking into account previous ASF modelling studies, which have applied a variety of assumptions and definitions. To provide context, Table 6 summarises the parameters employed in several major epidemiological modelling studies of ASF in wild boar populations. The table highlights differences in cell size, total number of cells, and how home ranges and contact between groups were defined. Considering these differences was important in developing the present model, as it illustrates the complexities of translating ecological and epidemiological assumptions into a spatially explicit, individual-based framework. This comparison situates the present model within the broader literature and highlights the diversity of approaches across studies.

Table 6. Spatial and demographic parameters used in previous ASF modelling studies of pig group distribution, highlighting differences in cell size, total cell numbers, and assumptions about home ranges and contact with neighbouring groups.

	Lange & Thulke (2017)	Halasa et al. (2019)	Salazar et al. (2022)	Croft et al. (2019)
Cell size	9 km2 (3 × 3 km)	4 km2 (2 × 2 km)	9 km2	approximately 4 km2
Total cell numbers (whole landscape)	10000 cells (approx. 200 × 200 km along the border between Estonia and Latvia)	about 23,000 cells (Denmark excluding the Island of Bornholm)	Two regions in France: 1) 1383 cells (12447 km2) 2) 972 cells (8748 km2)	NA (25 km buffer around the Forestiry Commission estate in the Forest of Dean)
How to divide the land into cells	By rastering to a specific cell size.		Rastering with habitat suitability classification	Edge of cells were defined by landscape barriers (e.g., calals, rivers more than 10 metres wide and major roads)
Number of neighbouring cells	8	8	8	Depends on the cell
What each cell represents	Home range of a single group. Functional classification of a landscape denoting habitat quality that is interpreted as breeding capacity at run time.	Home range of a single group. Categorized based on the forest coverage and habitat requirement threshold: 1) suitable habitat, 2) unsuitable habitat but accessible, and 3) unsuitable and inaccessible		A single realisation of how space could exist in the real world: patches here do not necessarily define the home range of an individual. A scale sufficient to host 20–30 boar per patch
Contact with pigs in other groups	Pigs in neighbouring groups could have contact in "connecting edge"(space between core habitat areas that is shared among neighbouring groups).		Contact could be made with neighbouring groups.	Contact could occur in overlap between neighboring groups (1.35km either side of a boundary line)

Epidemiological parameters of ASF

Transmission rate

Transmission rates were adapted from Lange (2015). These are commonly used in ASF wild boar models, as they were originally derived from best-fit models explaining observed spatial spread. As the epidemiological dynamics in this model are updated daily, the rates were taken from Salazar et al. (2022), who converted the weekly rates in Lange (2015) to daily rates.

Latent period and infectious period

The parameters for these periods were adopted from Halasa et al. (2019), who cited the results of the ASFV transmission experiment by direct contact of infected pigs with ASFV isolates from Poland conducted by Olesen et al. (2017).

Carcass persistence

This parameter was taken from Croft et al. (2020). It was derived from an annual field observation experiment of wild boar carcasses in Germany by Probst et al. (2017), reflecting the time it takes for scavengers to completely consume the carcasses.

Technical details of the model

The model was initially set up with a geographical range over which the model was to be run, which was then divided into contiguous cells. Each cell was numbered and assigned x- and y-values. The number of feral pigs was determined by specifying the number of cells occupied by feral pigs and the group size.

Population dynamics

Demographic processes were updated on a weekly basis. Each animal was represented by a randomly assigned individual ID, cell ID and its corresponding x y location, randomly assigned age, sex and life stage in the proportions shown in Table 4, dispersal step count, and epidemiological status. To represent the demography of feral pigs, each pig was probabilistically selected for natural mortality once a week. Those selected for natural mortality and those that reached their lifespan were removed from the model and replaced by a new susceptible piglet to maintain population size in the absence of disease. Once a week, male juveniles who had not reached the maximum dispersal step were instructed to take a total of 12 steps (24 km) in a random direction for each step. Once the weekly dispersion was over, 12 steps were added to the dispersion step count.

Dynamics of ASF

As ASF disease status can progress in short units of less than a week, the model was run on a daily basis with stochastic updating of disease progression, while demographics were updated weekly. ASF was assumed to be transmitted by: (i) direct contact with infected feral pigs within a group and (ii) contact with infected carcasses within a group or in neighbouring cells. Contact with live infected feral pigs was assumed to occur only within the group, as feral pigs have extensive habitat overlap between group members, but little overlap with those outside the group (Pepin et al., 2016). Transmission through carcasses was assumed to occur not only within the group, but also to feral pigs in neighbouring cells, as the range of feral pigs in this model setting could overlap with neighbouring cells, and wild boar were observed to have frequent contact with boar carcasses and softened soil near carcasses (Probst et al., 2017). Infected carcasses remained in the environment for a period of time (Table 4) and were then removed from the simulation to be replaced by new susceptible piglets. The disease course of each individual was updated daily according to the SEIR model, with the epidemiological parameters shown in Table 4.

The daily probability that a susceptible feral pig in a group (*g*) becomes infected by direct contact with an infected individual in the same group at the timestep t was adapted from Salazar et al. (2022) and calculated as follows:

$$PIL(g)(t) = 1 - (1 - P_{fl})^{N_{fl}^{(g)}(t)}$$

where P_{fl} is daily ASF infection probability by direct transmission from live feral pigs within group, and $N_{fl}^{(g)}(t)$ is the number of infected feral pigs in the group (*g*) at the time step (*t*), assuming homogenous and random mixing (i.e., each susceptible has an equal chance of being exposed to an infectious individual).

The daily probability that a susceptible feral pig in a group (g) becomes infected by contact with an infectious carcass in the same group or in a neighbouring cell at timestep t was adapted from Salazar et al.(2022) and calculated as follows:

$$PIC(g)(t) = 1 - \left(1 - P_{fc}\right)^{N_{fc}^{(g)}(t)} * \left(1 - P_{fcn}\right)^{N_{fc}^{(gn)}(t)}$$

where $P_{fc}$is daily ASF infection probability via infectious carcasses within group, and $P_{fcn}$is daily ASF infection probability via infectious carcasses in neighbouring cell. $N_{fc}^{(g)}(t)$ is the number of infectious carcasses in the group (g) at the time step (t), and $N_{fc}^{(gn)}(t)$ is the number of infectious carcasses in the neighbouring cells (gn) at the time step (t).

When a susceptible individual had contact with an infectious individual, they became exposed with probability as described above. The individual then became infectious after an average latent period of 5 days. Infected individuals became a source of infection in the group. The probability of mortality following infection was high (Table 4). Carcasses were retained for 56 days and could transmit the virus. Recovered individuals were not reinfected and were replaced by new susceptible piglets.

Farm-level visit and observation model

In addition to simulating ASF dynamics within feral pig populations, I developed a complementary farm-level model to evaluate the frequency with which domestic pig farms were visited by feral pigs and the probability that such visits would be detected. Farms were randomly distributed across the simulated landscape according to the density of pig holdings in Dumfries & Galloway (147 farms over 6,426 km^2; Scottish Government, 2024; UK government, 2023), ensuring that no farm was placed within a feral pig group's core cell.

Neighbouring farms were defined as those located within a Chebyshev distance of ≤1 cell (i.e. adjacent or diagonally adjacent cells) from feral pig groups. Each farm was assigned a daily visit probability conditional on the presence of nearby groups. To account for uncertainty in true visit probabilities, we evaluated scenarios ranging from 0.0025 to 0.04

visits per farm per day. For each scenario, we simulated visits to farms over a one-year period across 500 stochastic replicates. The simulated number of visits (V) was compared with the survey-derived estimate of annual visits (k_obs), and the required observation probability (p_obs) was calculated as k_obs / V. Maximum likelihood estimation was then applied to infer p_obs under each scenario, yielding relative likelihood profiles.

From these analyses, we summarised both the estimated observation probabilities and the proportion of farm visits that may have gone undetected under current surveillance.

Simulations

The model was developed and run using R version 4.4.3 (R Core Team, 2025). Initially, the population dynamics were run for 10,000 days without the introduction of ASFV to ensure that the population dynamics were stable. The following scenarios were then run:

Infection dynamics of ASF

One infected feral pig was introduced on day one and the model run for a year under population density of 1 head/ km^2 with 1000 iterations to estimate the infection peak, persistence of infection, and timing of transmission between individuals and groups.

Persistence of ASF

Five infected feral pigs were introduced on day one and simulations run for a range of assumed pig densities (0.01875, 0.025, 0.05, 0.125, 0.25, 0.5, 1, 2 head/km^2) to evaluate the persistence of infection. For scenarios with a density below 0.05, the landscape area was doubled (40km × 40km) and 100 iterations run to mitigate the impact of the low total pig population within the simulation area and to reduce the effects of stochastic fluctuations in small populations.

Farm visit and observation

Pig farms were placed within the landscape and simulations run under different visitation probabilities per feral pig group (0.0025, 0.005, 0.01, 0.02, and 0.04 times/day/farm) for 500 stochastic iterations over one year each, to estimate the probability of a visit being observed given the observation rates found in the earlier chapter.

Results

Examining ASF dynamics

Overview of average infection dynamics

A total of 500 simulations were conducted under steady-state population conditions of one feral pig per square kilometre to examine the progression of infection over one year following the introduction of a single infected feral pig. The results indicate that infection spread rapidly, reaching its peak at day 73 (median; mean 86.5 days, SD 54.0), and then tended to persist at a relatively low prevalene (approximately 5 to 10 %) thereafter (Figure 8a). The infection dynamics consisted of two segments of different infection phases – that is, an epidemic period (around 1-100 days), during which infection spreads rapidly and susceptible individuals decrease sharply in the early stages of outbreak, followed by an endemic period (from around 100 days), during which the number of susceptibles remains stable. From the time of introduction until around day 150, the number of susceptible individuals dropped from 400 to below 100, while the number of infected carcasses rose to above 250. The number of exposed and infected individuals temporarily increased in the early phase, subsequently declining and levelling off at a low level, but did not reach zero. A small proportion of simulations did not result in an outbreak (Figure 8b, grey dots).

Variation in simulation outcomes

In the majority of simulations, the number of carcasses increased rapidly, particularly within the first 100 days following the introduction of an infected individual (Figure 8c). From around day 150 onwards, the number of carcasses tended to plateau, stabilising at approximately 250 to 320, indicating a balance between new infections and carcass decay or replacement. Conversely, several simulations showed minimal increases in carcasses, remaining close to the baseline, suggesting that the infection failed to spread beyond the initial case. This range of outcomes may represent the distinction between scenarios of sustained transmission and early fade-out. This observation is explored further in the subsequent section.

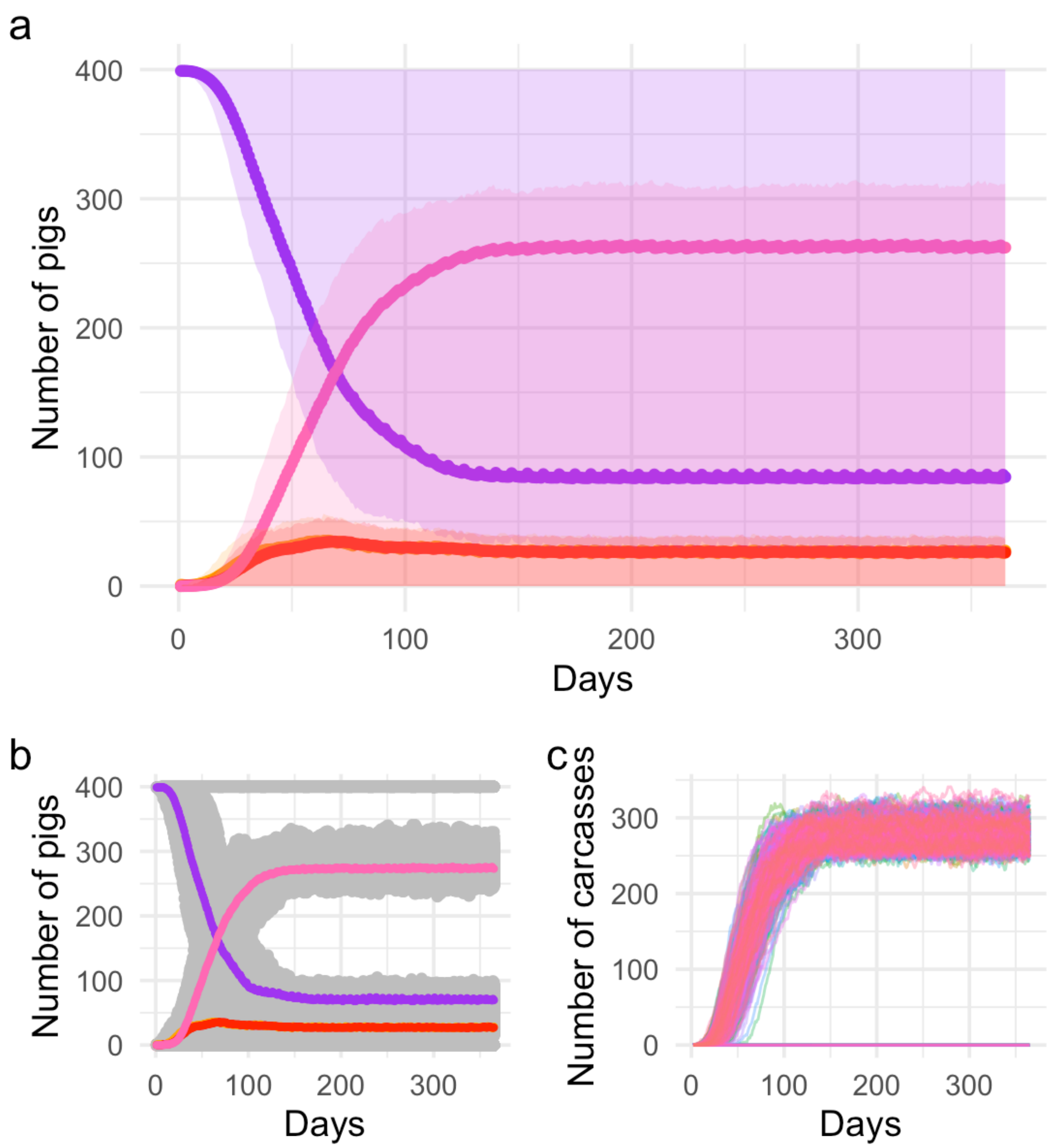

Figure 8. One-year infection dynamics of African swine fever (ASF) in feral pig population at a density of 1 pig per km² following the introduction of a single infected individual.

(a) Mean infection trajectory across 500 simulations. Dynamics are shown for susceptible pigs (purple lines), exposed pigs (orange lines), infectious pigs (red lines), and carcasses (pink lines). The shaded area represents the 95% confidence interval. (b) Median infection trajectory across 500 simulations. Colours are the same as in (a). Grey dots show the results of all 500 simulation runs. (c) Variation in carcass numbers across 500 simulations. Each simulation represented by a different colour.

Persistence of infection

Of 500 simulations, 25 (5.0%) resulted in natural fade-out without reaching a large-scale outbreak. Fade-out was defined as occurring when the number of infected individuals at the peak of the infection remained below 10. In the remaining 95.0% of simulations, the infection did not subside during the year-long simulation period.

Time to second case and spread to another group

Of 500 repetitions, infection spread to a second pig in 476 cases (95.2%), 78.8% (375 cases) of which occurred within two weeks. When infection spread, the median time from the introduction of the initial case to the identification of the second case was 9 days, with an average of 10.6 days (standard deviation ± 5.8 days) (Figure 9a). Transmission to the second group occurred in 95% (475 cases), with 92% (437 cases) occurring within three weeks. The median time to infection in the second group was 11 days, with an average of 12.2 days (standard deviation ± 6.4 days) (Figure 9b). In all instances where transmission to other groups occurred, the infection became established. In contrast, when no between-group transmission took place, establishment of infection did not occur (Figure 10).

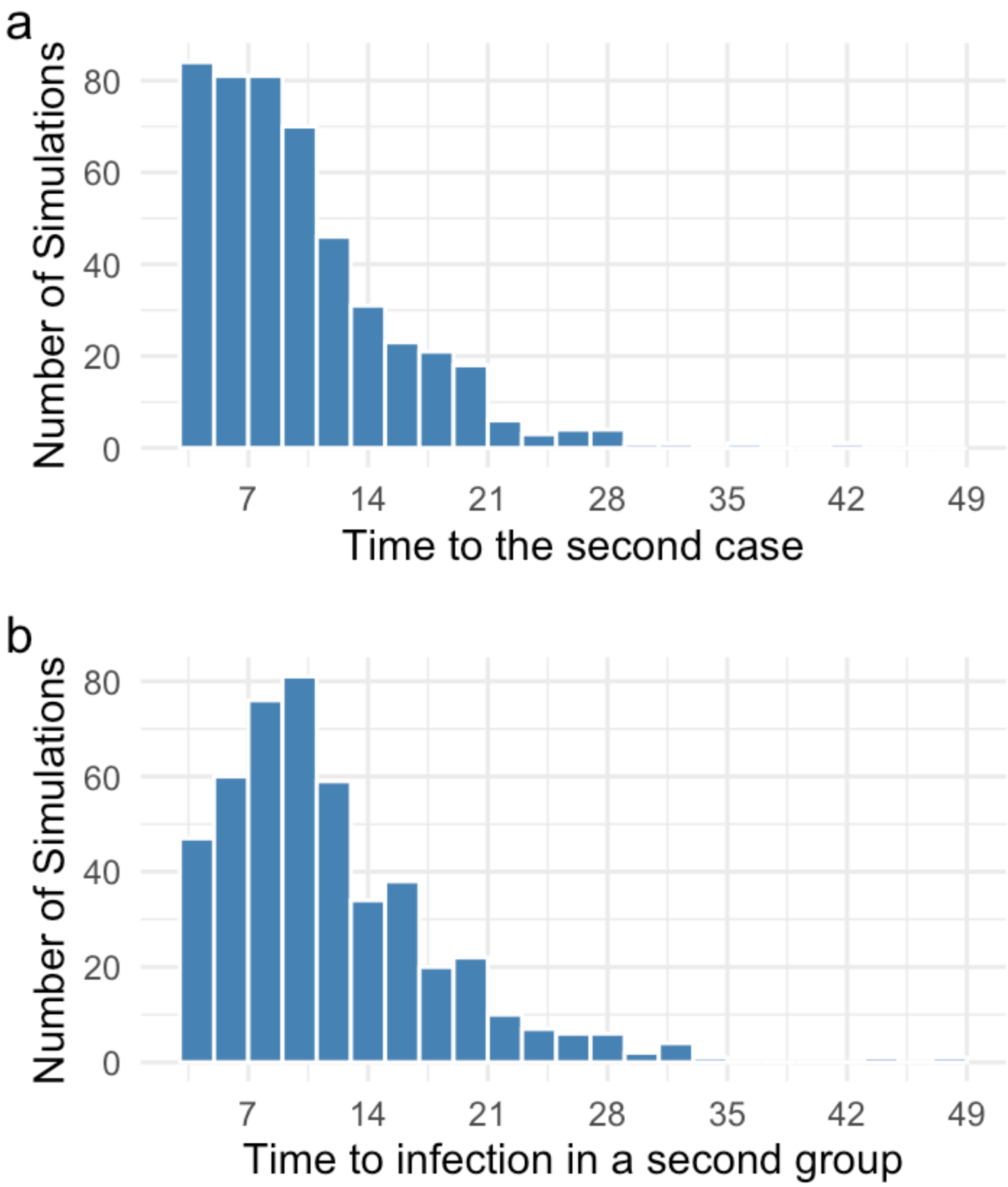

Figure 9. Time until infection spread to a second individual and to a second group in feral pig population.

Results are based on 500 simulation replicates following the introduction of a single infected individual at a density of 1 pig per km². (a) Distribution of the number of days until a second infection occurred. Simulations without a confirmed second infection (n = 24) were excluded. (b) Distribution of the number of days until infection spread to another group. Simulations without a confirmed secondary group infection (n = 25) were excluded.

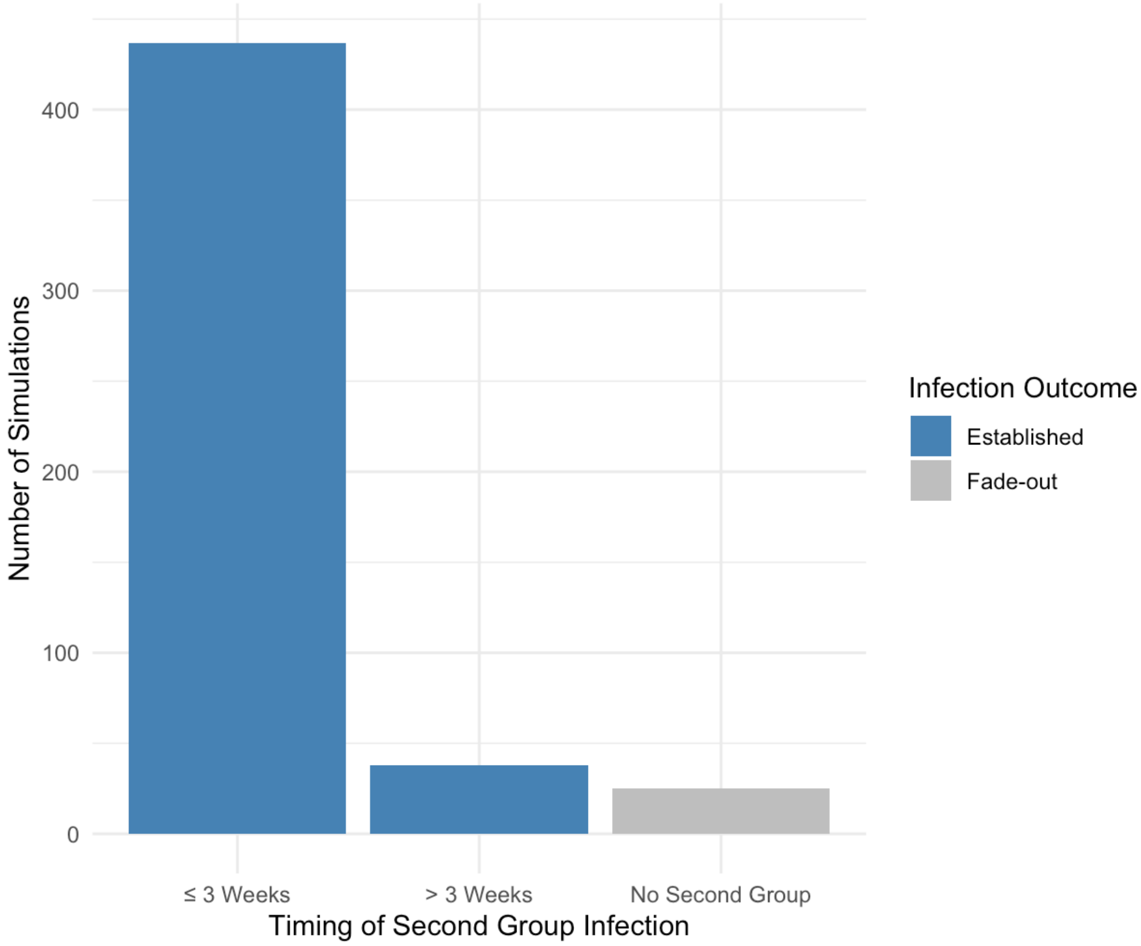

Figure 10. Distribution of infection outcomes (established or fade-out) by the timing of the second group infection.

Results are based on 500 simulation replicates following the introduction of a single infected individual at a density of 1 pig per km².

Peak infection period and scale of epidemic

Excluding the 25 simulations that suffered fade-out, the median time to reach the peak was 73 days, with an average of 86.5 days (standard deviation ± 54.0 days) (Figure 11). Although this period varied, peak infection was most commonly observed between days around 50 and 100. 76% (380 cases) reached their peak by day 100. At the peak, the maximum number of infected individuals was 70, representing 17.5 % of the total population. Excluding fade-out instances, the median cumulative number of infected animals during the period was 2,023, with an average of 2,041.6 (standard deviation ± 115.5).

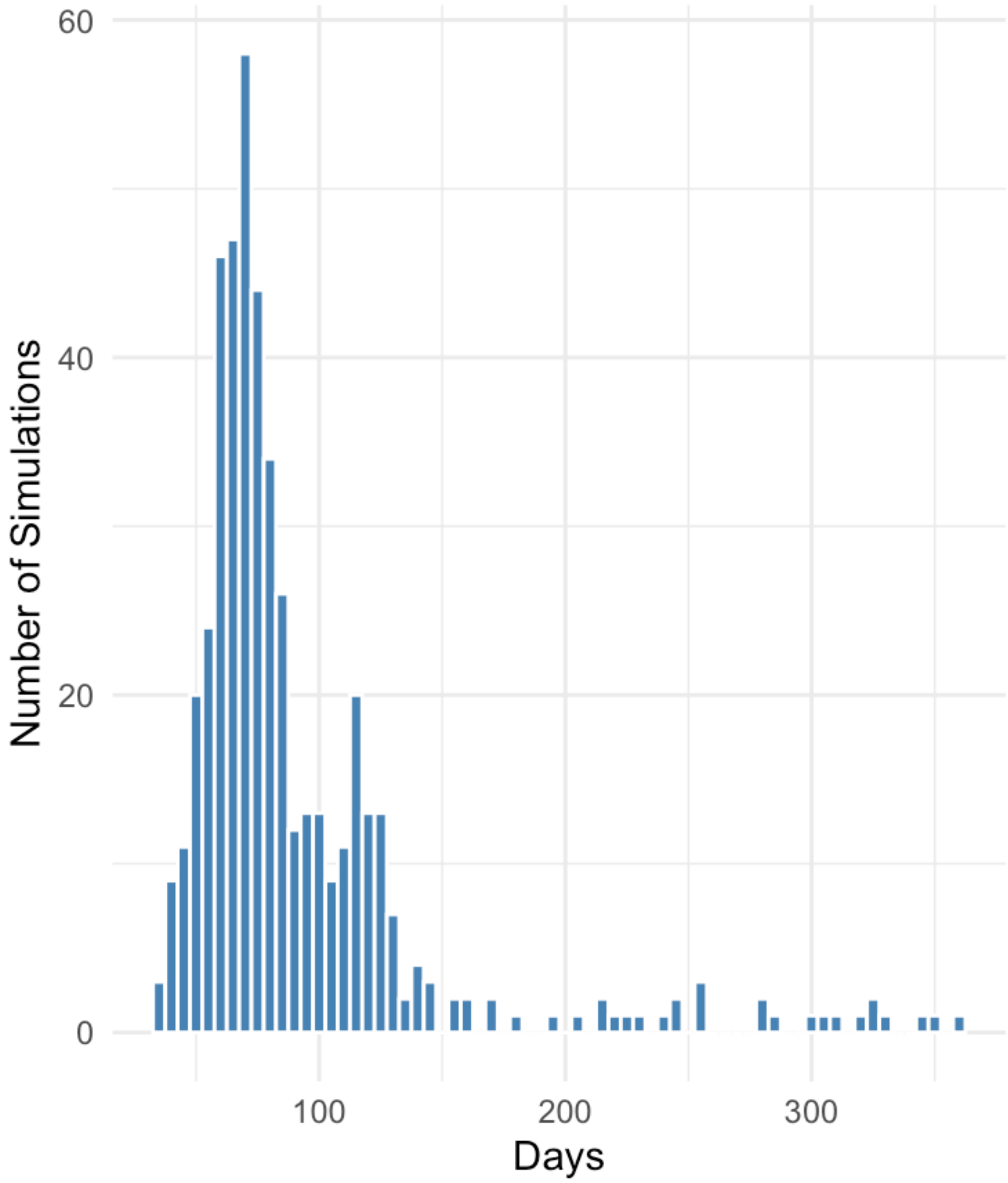

Figure 11. Distribution of days taken to peak infection.

Results are based on 500 simulation replicates following the introduction of a single infected individual at a density of 1 pig per km². Repetitions where a second infection was not confirmed (n=15) were excluded from the plot.

Examining ASF persistence

One-year simulations were conducted to examine the population density required for ASF persistence, starting from five infected individuals under varying population densities. Infection persisted in most simulations, even at very low population densities (Table 7), with fade-out observed only at densities of 0.01875 head/km² (4%) and 0.025 head/km² (2%).

The final proportion of susceptible individuals generally decreased with increasing population density (Table 7). Specifically, at 0.05 head/km², the final proportion of susceptibles was 0.56; at 0.5 head/km², it was 0.405; and at 2 head/km², it decreased to 0.024. At very low densities, the relationship between population density and the final proportion of susceptibles was harder to discern due to the stochasticity in outcomes.

Table 7. Outcome of ASF simulations under varying population densities.

Population density (head/ km²)	**0.01875**	**0.025**	**0.05**	**0.125**	**0.25**	**0.5**	**1.0**	**2.0**
Repetition	100	100	100	—	—	—	—	—
Area (km²)	40*40	40*40	40*40	20*20	20*20	20*20	20*20	20*20
Proportion of occupied cells	0.0075	0.01	0.02	0.05	0.1	0.2	0.4	0.8
Number of cells	400	400	400	100	100	100	100	100
Number of occupied cells	3	4	8	5	10	20	40	80
Number of pigs	30	40	80	50	100	200	400	800
Proportion of Infection establishment	**96%**	**98%**	**100%**	**100%**	**100%**	**100%**	**100%**	**100%**
Final proportion of susceptibles	0.398	0.298	0.56	0.42	0.39	0.405	0.105	0.024

Footnote: —, not applicable.

Figure 12 illustrates the infection dynamics across different population densities. At high densities (1–2 head/km²), infection spread rapidly, infecting most individuals within a short period and resulting in a very low final proportion of susceptibles. In contrast, at moderate to very low densities (0.01875–0.5 head/km²), infection initially increased rapidly, then stabilized, leading to an intermediate reduction in the proportion of susceptible individuals.

These observations indicate that ASF can persist across a wide range of population densities, even under very low densities, with the extent and speed of infection spread varying according to density.

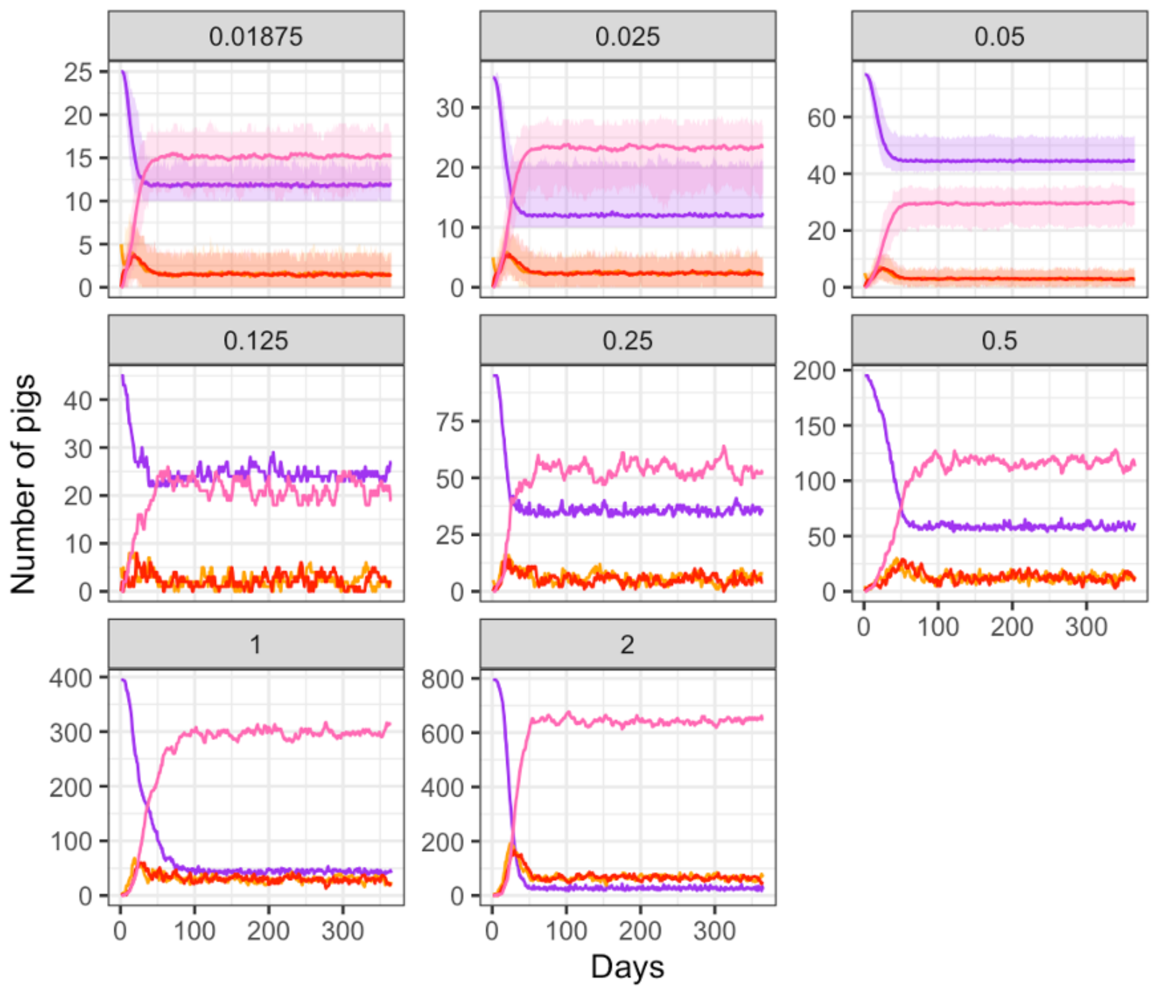

Figure 12. Infection dynamics over one year starting with five infected feral pigs at population densities from 0.01875 pigs per km² to 2 pigs per km².

Dynamics are shown for susceptible pigs (purple lines), exposed pigs (orange lines), infectious pigs (red lines), and carcasses (pink lines). Note that the number of feral pigs (y-axis) varies at every population density. Scenarios below a density of 0.05 are presented as the averages of 100 repetitions to mitigate the stochasticity in small populations, along with 95% confidence intervals. Densities above this level are based on a single simulation. Study area was doubled (40km × 40km) for densities below 0.05 to reduce the impact of low total pig numbers in the simulated area.

Farm visitation by feral pigs and observation probabilities

Nine farms were allocated within the simulated landscape, based on farm density calculated from official statistics for Dumfries and Galloway. All nine farms had at least one feral pig group located in an adjacent grid cell. As shown in Figure 13, because feral pigs live in groups, local clusters emerged even under the assumed overall density of one pig per km², resulting in heterogeneity in density across grid cells. The median annual number of visits per farm increased with the assumed daily visit probability, ranging from approximately one to 15 visits (Table 8).

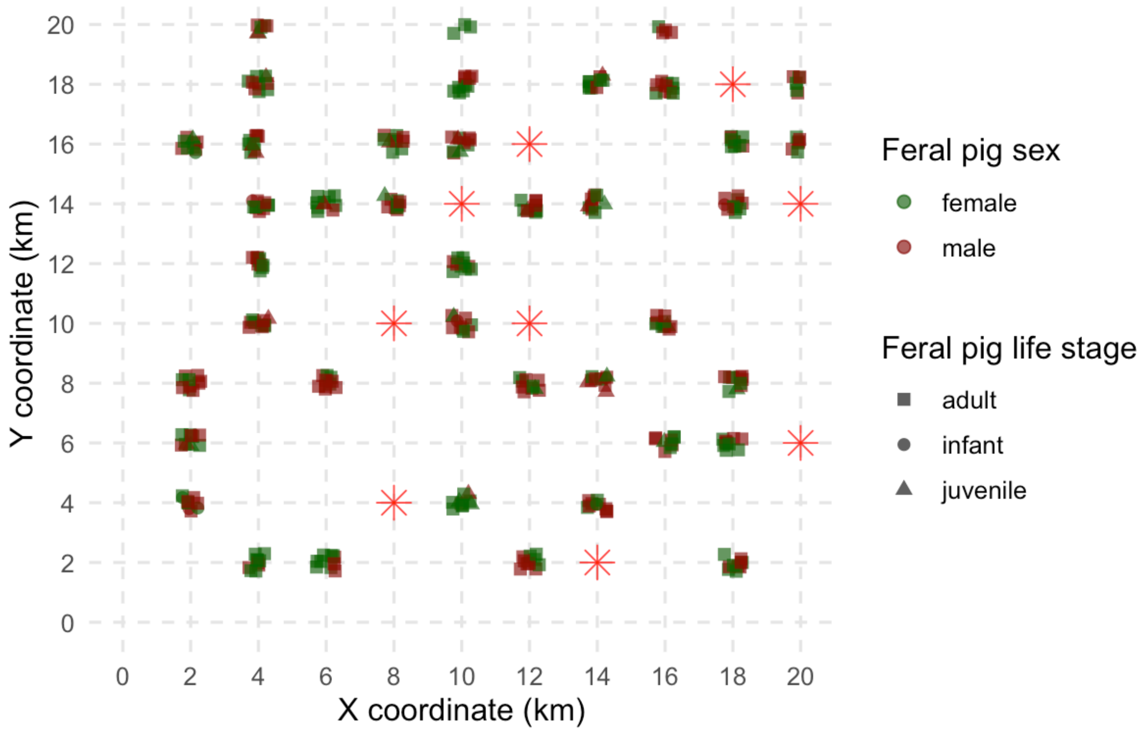

Figure 13. Locations of feral pigs and pig farms in the simulated landscape. Feral pigs were simulated at a density of one pig per km². Each point represents an individual feral pig, colored by sex (male/female) and shaped by life stage (infant, juvenile, adult). Red stars indicate pig farms. Each grid cell corresponds to 2 km × 2 km. Farms located within 1 grid cell (2 km) of a feral pig group are considered "nearby" and are potentially at risk of visits. The daily visit probability per pig group was set to a uniform value based on survey data.

Table 8. Annual number of visits to pig farms under different visit probability scenarios.

The median total annual visits across all farms with nearby feral pig groups, as well as the median annual visits per farm (with 95% confidence intervals) are presented. Values were obtained from 500 simulation replicates over a 365-day period. Farms were considered to have nearby pig groups if at least one feral pig group was located within the same or an adjacent 2-km grid cell (Chebyshev distance ≤ 1).

Visit probability scenario (per group)	Total annual visits (total of 9 farms)	Annual visits per farm
0.0025	8	0.89 (0.33–1.56)
0.005	16	1.78 (0.89–2.67)
0.01	33	3.67 (2.56–4.95)
0.02	67	7.44 (5.67–9.11)
0.04	132	14.67 (12.28–17.00)

At the farm level, the required observation probability (p_obs) decreased as the assumed daily visit probability increased (Figure 14a). Under the scenario with the lowest visit probability (0.0025), the median p_obs was approximately 0.6, whereas for scenario with higher visit probability (0.02–0.04), the median p_obs was below 0.1. Further analysis using maximum likelihood estimation indicated that p_obs values consistent with the observed data ranged between 0.05 and 0.6 across scenarios (Figure 14b).

Figure 14. Observation probability (p_obs) across different visit probability scenarios fitted to observed data.

Values are derived from 500 simulation replicates. (a) Boxplot showing distribution of required p_obs for each scenario. (b) Relative likelihood curves for each scenario, with red dots indicating the MLE.

The missed fraction of farm visits increased with higher assumed visit probabilities (Table 9). At a daily visit probability of 0.0025, the median missed fraction was 0.375 (95% CI: –0.667–0.643), whereas at a probability of 0.04, the missed fraction reached 0.962 (95% CI: 0.955–0.967). This pattern reflects that under higher visit probabilities, a smaller proportion of visits would need to be observed to match the survey data.

Table 9. Required observation probability (p_obs) and missed fraction (1 – p_obs) across visit probability scenarios.

For each assumed visit probability scenario, the table presents the median and 95% confidence interval of the probability that a visit of a feral pig group to a farm would be observed (p_obs) and the corresponding missed fraction. Values are based on 500 simulations.

Visit probability scenario (per group)	Required observation probability (p_obs)	Missed fraction (1 – p_obs)
0.0025	0.625 (0.357–1.667)	0.375 (-0.667–0.643)
0.0050	0.312 (0.208–0.625)	0.688 (0.375–0.792)
0.0100	0.152 (0.112–0.217)	0.848 (0.783–0.888)
0.0200	0.075 (0.061–0.098)	0.925 (0.902–0.939)
0.0400	0.038 (0.033–0.045)	0.962 (0.955–0.967)

Discussion

Key findings

The results of this study can inform contingency planning for feral pigs in Scotland. Three main findings emerged from the modelling investigation.

Firstly, the persistence of infection was strongly associated with the occurrence of between-group transmission. The occurrence of between-group transmission reflects threshold conditions for persistence, with most instances occurring within three weeks of initial introduction. Once established, ASF tended to persist over long periods, even after the initial peak of infection. These results suggest that the first few weeks following introduction are critical in determining whether ASF fades out or becomes endemic. Similar observations have been reported in previous studies. For instance, EFSA (2018b) concluded that the persistence of ASF in wild boar populations largely depends on the speed and extent of spread immediately following introduction. They emphasised that rapid containment of initial clusters is crucial. Likewise, analysis of ASF introduction cases in Germany by (Lentz et al., 2023) demonstrated that infection spread rapidly in both temporal and spatial dimensions immediately after the initial outbreak, and that this early spread pattern influences the subsequent persistence of the outbreak.

Secondly, ASF was shown to persist in feral pig populations even under conditions of very low population density. Even at densities as low as 0.01875–0.025 heads/km², infection persisted in most simulations, with fade-out being observed rarely. This finding is consistent with existing reports indicating that ASF can persist without a clearly defined density threshold, being maintained through routes such as indirect transmission via infectious carcasses (EFSA, 2018b). EFSA (2018b) further notes that, while density is the most important risk factor for the occurrence of ASF in wild boar, persistence cannot be explained by density alone. Complex factors, such as transmission via infectious carcasses and spatial structure, also play a role.

Thirdly, the analysis of farm-level visit probabilities indicates that the observed survey data can be explained by different combinations of visit and observation probabilities. The observed visit frequency was 0.0016 visits per farm per day (Table 3). Comparing this with simulation results, under infrequent visit scenarios (daily visit probability per group = 0.0025), a relatively high observation probability (median ≈ 0.63) is required to reproduce the survey data, whereas for intermediate (0.01/day) or frequent (0.04/day) visits, the required observation probability decreases to ≈ 0.15 and ≈ 0.038, respectively (Table 9). These patterns suggest that if visits are frequent, only a small fraction needs to be observed to match the survey data, whereas for rare visits, a higher observation probability is necessary. Therefore, the low observed visit frequency may reflect genuinely low visit activity, incomplete detection (i.e., under-reporting), or a combination of both. These results highlight the uncertainty in interpreting observed visit frequency and the importance of considering the possibility of both low visit frequency and limited detectability when evaluating report-based farm-level exposure.

Taken together, these findings suggest that, in Dumfries & Galloway, ASF could persist across a wide range of feral pig population densities, provided that transmission between groups occurs in the early stages. These results have direct implications for risk management, particularly emphasising the importance of rapid detection and removal of infectious carcasses, as well as containment measures, during the first few weeks after introduction, in order to limit further spread. Preventing or delaying transmission between social groups could substantially reduce the likelihood of long-term persistence. Furthermore, ASF's ability to persist even at low densities emphasises that reducing population density alone may not eliminate infection, highlighting the need for continued long-term surveillance and management. The timing of the first transmission between groups may be a useful indicator of the potential for ASF persistence. Moreover, the observed low frequency of farm visits by feral pigs should be interpreted with caution, as it may reflect either genuinely rare visits, under-reporting due to limited detectability, or a combination of both. Recognising this uncertainty is essential when evaluating farm-level exposure in scenario analyses and when designing effective surveillance and biosecurity strategies. These findings are important as they can improve scenario assessments regarding ASF invasion and spread, and contribute to strengthening surveillance systems in contingency plans and prioritising biosecurity measures on farms.

Limitations

Several limitations should be noted. The simulation was conducted under the simplified assumption of a constant population size, without accounting for demographic fluctuations or spatial heterogeneity. Consequently, the potential for fade-out due to the depletion of susceptible individuals may be underestimated. Furthermore, only direct and indirect transmission via infectious carcasses were considered; long-distance transmission via humans or fomites was not incorporated. While the role of persistently infected wild boar remains debated, the current literature provides insufficient evidence to suggest that they play a significant role (Blome et al., 2020; Ståhl et al., 2019). The two primary transmission routes considered in this model — direct transmission via infected individuals and indirect transmission via infectious carcasses — have been shown to be sufficient to explain the long-term survival and continued spread of ASFV in low-density environments in continental Europe (Gervasi & Guberti, 2021).

Seasonality was not incorporated into the model. During the breeding season, the addition of newborn piglets to the susceptible population can rapidly increase the number of infected individuals, thereby raising the risk of direct transmission (Guberti et al., 2019). Transmission via infectious carcasses is also likely to be affected by seasonal variation: field studies in Germany have shown that the process of skeletonisation of wild boar carcasses takes longer in winter, while carcass contact occurs most frequently in summer and autumn (Guberti et al., 2019; Probst et al., 2017). Such seasonal variations may influence the rate and persistence of infection, but they were omitted from this study for simplicity.

Geographical factors were also not considered. It is known that landscape structure, habitat fragmentation and forest density influence the spread of ASF (Salazar et al., 2022). As the study area consists primarily of grassland and woodland, and the modelled area is relatively small (20×20 km^2), the impact of geographical conditions was deemed minimal. However, for future large-scale simulations, it will be important to incorporate habitat and landscape features in order to make a more accurate assessment of ASF transmission dynamics.

Additionally, the population density of feral pigs in Scotland is unknown. For this study, a density of one pig per km^2 was assumed based on EU data. However, uncertainties in density estimates due to regional differences have been noted even for wild boar populations across the EU (EFSA, 2018b, 2022).

Future Directions

Future research could aim to reduce these uncertainties and enhance the realism of the model. In particular, obtaining reliable field data on feral pig density, distribution, population size, and carcass persistence in Scotland would be valuable. Incorporating seasonal variation and spatial structure, including habitat and landscape characteristics, into the model may allow a more regionally specific understanding of long-term infection persistence.

Chapter 5 Discussion

Background and importance

African swine fever (ASF) is recognised as one of the most serious threats to domestic pigs and wild suids worldwide, with devastating economic and animal health consequences (EFSA, 2018a). In continental Europe, wild boar have been identified as key drivers of ASF transmission and persistence, with evidence for both direct contact and indirect transmission via infectious carcasses (Gervasi & Guberti, 2021; Probst et al., 2017). Although ASF has not yet occurred in Scotland, the presence of feral pigs—whose numbers may increase—represents a major potential risk factor for ASF incursion. Consequently, reliable data on their distribution and abundance are indispensable for designing preventive strategies and contingency plans. However, as demonstrated in Chapter 1, the available data are limited and lack consistency. The primary source, the NBN Atlas, relies heavily on voluntary reporting, with considerable variation in time periods and reporting criteria, making accurate population estimates difficult. This highlights the urgent need for standardised and systematic monitoring.

Empirical evidence of feral pig–domestic pig interactions

In Chapter 2, preliminary insights were presented regarding interactions between feral pigs and outdoor-reared domestic pigs in Scotland. Although direct observations or contacts were reported by only a minority of surveyed farms, the accounts of multiple feral pigs visiting simultaneously indicate that such interactions do occur and may facilitate pathogen transmission. These interactions were broader in scope than previously reported, encompassing exploratory and aggressive behaviours. The discrepancies observed between survey reports and official NBN records further imply that the presence of feral pigs may be underestimated. While limitations such as small sample size and potential observation bias should be acknowledged, these findings underscore the need to consider multiple pathways of contact in ASF risk assessments (EFSA, 2021).

Model-Based Risk Assessment and Implications

Chapter 3 used simulation models to assess ASF dynamics under various scenarios. Three key findings emerged: (1) the occurrence of between-group transmission may represent a threshold condition for the establishment of infection, with the first few weeks following introduction being particularly critical; (2) ASF can persist even at very low feral pig densities due to indirect transmission via carcasses, indicating that reducing population density alone may not prevent infection; and (3) Careful interpretation is required when incorporating empirical observations into risk assessment, surveillance, and contingency planning. These results underscore the importance of rapid detection, removal of infectious carcasses, and containment measures in the early stages of an outbreak.

Limitations and Future Directions

Across all chapters, several limitations should be noted: limited and heterogeneous population data, simplified modelling assumptions (constant population size, limited transmission routes, no seasonality or spatial heterogeneity), and survey constraints including small sample size and self-selection. Future research should aim to obtain more regionally specific insights for Scotland by implementing standardised field monitoring, including camera traps, thermal imaging, and hunting records; incorporating seasonal and spatial variation into models; and improving farm-level surveillance to better estimate the true frequency of feral pig–domestic pig interactions.

Conclusions and Implications

Integrating findings from all chapters provides a comprehensive understanding of ASF risk in Scotland and highlights key knowledge gaps. Reliable feral pig population data are urgently needed. Feral pigs may visit pig farms in groups, and even limited interactions between feral pigs and domestic pigs can pose a potential risk for ASF transmission. Once ASF spreads within a feral pig population, the infection can be maintained even under very low population densities. Effective management requires a combination of data collection, early detection and carcass removal, and biosecurity interventions to prevent disease introduction and limit long-term persistence. This study highlights the complex interactions between feral pig ecology, farm management, and disease dynamics, providing critical insights for contingency planning and biosecurity prioritisation.

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