

The European Wild Boar (*Sus scrofa*) as a Reservoir of Tuberculosis: Ecological Drivers and Management Implications

¹Giovanna Liguori, ¹Renato Lombardi, ²Fabio Castagna, ²Roberto Bava, ³Nadia Piscopo, ⁴Massimiliano Quintiliani, ⁴Margherita D'Angelo, ⁵Grazia Matarante, ³Anna Costagliola, ²Ernesto Palma, ²Domenico Britti and ^{6,7}Antonio Giordano

¹Local Health Authority, ASL, 71121 Foggia, Italy

²Department of Health Sciences, University of Catanzaro Magna Græcia, 88100 Catanzaro, Italy

³Department of Veterinary Medicine and Animal Productions, University of Napoli Federico II, 80100, Naples, Italy

⁴Sbarro Health Research Organization ETS, 10060, Candiolo (TO), Italy

⁵Local Health Authority, ASL, 86100, Molise Region, Campobasso, Italy

⁶Department of Biology, Sbarro Institute for Cancer Research and Molecular Medicine, Center for Biotechnology, College of Science and Technology, Temple University, Philadelphia, PA, USA

⁷Department of Medical Biotechnology, University of Siena, 10100, Siena, Italy

Article history

Received: 06-12-2024

Revised: 01-05-2025

Accepted: 20-05-2025

Corresponding Author:

Giovanna Liguori

Local Health Authority, ASL,
71121 Foggia, Italy

Email: giovanna.liguori@unina.it

Abstract: Bovine tuberculosis (bTB), an infectious disease primarily caused by *Mycobacterium bovis* and other members of the *Mycobacterium tuberculosis* complex, represents a significant challenge to both animal and public health. Despite successful control programs in numerous regions, the presence of wildlife reservoirs, notably wild boar (*Sus scrofa*), impedes complete eradication and sustains disease propagation. bTB prevalence varies across Europe, with higher rates in regions like southern Italy and Spain, influenced by intensive livestock systems, wildlife-domestic animal interactions, and environmental conditions favoring *Mycobacterium bovis* survival and transmission. Wild boar and other ungulates are key *Mycobacterium bovis* reservoirs, maintaining infection within wildlife and facilitating cross-species transmission to livestock. Shared grazing areas and resources exacerbate pathogen spread, highlighting the need for integrated control strategies addressing both wildlife and domestic animals. Effective bTB management requires a comprehensive approach encompassing surveillance, vaccination, and targeted control measures for both populations. This involves monitoring wildlife, implementing biosecurity protocols to minimize cross-species transmission, and exploring wildlife-specific vaccination strategies. In wild boar-prevalent regions, reducing their role as *Mycobacterium bovis* reservoirs is crucial to limit zoonotic and interspecies transmission. Understanding wild boar population dynamics and interspecies interactions is essential for ongoing efforts to control this zoonotic disease. This narrative review of the scientific literature will analyze these various aspects to provide a current picture of the situation. Meaningful solutions are proposed to reduce the risk associated with this phenomenon.

Keywords: Tuberculosis, Wild Boar (*Sus scrofa*), Animal Reservoir, Zoonosis Disease, One Health

Introduction

Tuberculosis represents a persistent and weakening zoonotic disease, incited by bacteria belonging to the *Mycobacterium tuberculosis* complex. This complex encompasses a group of

closely related mycobacterial species and ecotypes, demonstrating diverse pathogenicity and host specificity, and capable of infecting both humans and a variety of animal species (Barroso *et al.*, 2023; Gortazar *et al.*, 2005; Neill *et al.*, 2005). *Mycobacterium bovis* is the principal etiological

agent of bovine tuberculosis (bTB) in cattle. Ruminants like goats, along with swine and cattle, are vulnerable to *Mycobacterium bovis* infection, thereby posing considerable problems for both population-level health initiatives and animal healthcare practices (Amanfu, 2006).

Based on characteristic deletion patterns, four distinct clonal complexes of *Mycobacterium bovis* have been identified: African 1, African 2, European 1, and European 2. These complexes exhibit notable geographical structuring, with African 1 and 2 primarily confined to the African continent, European 2 frequently encountered in the Iberian Peninsula, and European 1 displaying a global distribution (Zimpel *et al.*, 2020). Caprine, porcine, and bovine species are all vulnerable to infection by *Mycobacterium bovis*, a susceptibility that presents significant consequences for both public health and animal healthcare systems (Amanfu, 2006).

Due to sustained control interventions, numerous nations are now recognized as bTB-free (European Food Safety Authority and European Centre for Disease Prevention and Control) (EFSA, 2018). Eradication programs are currently being implemented in countries with ongoing bTB prevalence, including several European nations, Japan, New Zealand, the United States, and select Central and South American nations (Humphrey *et al.*, 2014; Livingstone *et al.*, 2015; Shimao *et al.*, 2010).

The "test and cull" approach, utilizing single and comparative skin tests, along with IFN-gamma testing where necessary (Pollock *et al.*, 2006; Macdonald *et al.*, 2006), forms the foundation of national eradication efforts for *Mycobacterium bovis* in cattle and vulnerable animals. Despite intensive livestock eradication programs and the demonstrated effectiveness of skin tests in diagnosing TB in cattle, complete eradication has not yet been achieved (Amanfu, 2006; Pavlik, 2006). This incomplete success is largely attributed to the presence of *Mycobacterium bovis* reservoirs in wild animal populations (Amanfu, 2006; Thoen *et al.*, 2006; Morris *et al.*, 1994; Cousins *et al.*, 2001; Corner *et al.*, 2006; Collins *et al.*, 2006).

Tuberculosis cases have been documented in numerous European and overseas countries. The wild boar (*Sus scrofa*) has emerged as a critical maintenance host for the disease (Corner *et al.*, 1981; Bollo *et al.*, 2000; Naranjo *et al.*, 2008; Gortázar *et al.*, 2008; Palmer *et al.*, 2002). The disease in wild boar is caused by bacteria belonging to the MTBC

(*Mycobacterium bovis*, *Mycobacterium caprae*, *Mycobacterium microti*, etc.), which are capable of infecting a wide range of wild and domestic animals, as well as humans. *Sus scrofa* can sub-clinically spread the disease among animal populations over extended periods, triggering recurrent outbreaks in cattle. Wild boar has been shown to be highly susceptible to TB and reproduce some of the clinical signs observed in humans. Infection primarily occurs in the first months of life through oral-nasal routes, with the mandibular lymph nodes being the most frequently affected tissue through the formation of granulomatous lesions. This is possibly the main organ responsible for disease progression (i.e., the dissemination of infection throughout the organism).

Contemporary investigations reveal that tuberculosis represents roughly 30% (on average) of the aggregate mortality incidence in mature wild boar, implying a dimension of TB-mediated selection. Predation and inanition stemming from harsh environmental circumstances (e.g., arid, elevated-temperature seasons) also influence wild boar demise within Mediterranean ecosystems. The convergence of environmental stressors incited by arid, elevated-temperature seasons coupled with robust MTBC contagion pressure, arising from elevated population density/congregation and indirect interaction with MTBC via a tainted milieu (e.g., watering holes), renders these wild boar communities an unparalleled paradigm for comprehending host-pathogen dynamics (Queirós *et al.*, 2018). The ecological attributes of wild boar—omnivorous and necrophagous alimentary habits, communal conduct, and stable familial cohorts—augment its function as a disease sentinel, notably considering the species' continuous demographic augmentation, especially pertaining to hunting. *Sus scrofa* demonstrates the most expansive geographical dispersion amongst ungulates, encompassing five continents: Asia, Europe, Africa, America, and Oceania. Its proliferation has been notably pronounced throughout Europe in recent decades (Gortázar *et al.*, 2005).

Instances of wild boar tuberculosis have been documented across numerous European nations, with Mediterranean regions exhibiting particularly elevated prevalence rates. Mediterranean ecosystems are defined by desiccated summers, which leads to the natural concentration of animals around scarce water sources (Gortázar *et al.*, 2006). Molecular investigations corroborate the sharing of identical

MTBC genotypes between domestic and wild animals in these regions, providing unambiguous evidence of cross-species transmission (Gortázar *et al.*, 2006; Vicente *et al.*, 2006; Aranaz *et al.*, 1996; 2004). These transmission dynamics bear direct implications for human health, as the continuing global expansion and population growth of *Sus scrofa* increasingly brings these animal reservoirs into contact with human populations.

Consequently, this narrative literature review probes the ecological and epidemiological elements that position wild boar populations as significant amplifiers of *Mycobacterium bovis*. We investigate the mechanisms underpinning disease transmission between wild boar (wildlife) and domestic livestock, focusing on the zoonotic risks arising at wildlife-livestock interfaces. By synthesizing existing scientific evidence, we aim to elucidate the European wild boar's role in tuberculosis epidemiology, with the goal of pinpointing key knowledge gaps. The final section assesses limitations within current management strategies and proposes actionable One Health recommendations that integrate these epidemiological findings, thereby connecting wildlife management and human health protection. A thorough understanding of wild boar disease dynamics is crucial for developing effective control measures to reduce risks to both animal and human health.

Materials and Methods

To ascertain the role of the European wild boar (*Sus scrofa*) in the zoonotic transmission of *Mycobacterium bovis* and its potential as a reservoir host for bovine tuberculosis (bTB), a comprehensive review of the literature was undertaken. The following databases were queried to gather pertinent data: PubMed, Google Scholar, ScienceDirect, and Web of Science. The search strategy encompassed specific terms related to zoonotic diseases and wildlife reservoirs, including "wild boar," "*Sus scrofa*," "zoonosis," "meat," "*Mycobacterium bovis*," "bovine tuberculosis," "*Mycobacterium tuberculosis* complex," "MTBC," "wildlife," "reservoir host," "European wild boar," "tuberculosis," "animal reservoir," "zoonosis disease," "ruminants," and "livestock animal." These search terms were strategically combined using Boolean operators ("AND," "OR") to ensure a thorough coverage of the subject matter. The review focused primarily on peer-reviewed articles published in English. Studies addressing the epidemiology, transmission routes, clinical manifestations, and control measures of zoonotic

diseases principally associated with wild boar were given priority. Investigations into the impact of wildlife as a potential source of disease dissemination to livestock and human populations were also taken into account. The gathered literature was organized and assessed based on the quality of the evidence presented, with emphasis on studies that examined the transmission dynamics of *Mycobacterium bovis* within wildlife populations, particularly the European wild boar (*Sus scrofa*), and its implications for livestock and public health. Data from these sources were synthesized to provide a detailed overview of the role of wild boar as an animal reservoir in the context of zoonotic disease outbreaks, with a particular focus on tuberculosis and its impact on ruminants and other livestock animals.

Factors Affecting Mycobacterium Transmission and Persistence in Reservoir Hosts

Wild animal populations can exert a substantial influence on the epizootiology of bovine tuberculosis (bTB). For effective disease management, it is crucial to differentiate between maintenance and spillover hosts. Maintenance hosts are defined as those capable of independently sustaining infection within a specific geographic area, without requiring cross-transmission from other domestic or wild species. Conversely, spillover hosts, as described by Morris *et al.* (1994), depend on continuous infection from other species to perpetuate the disease. Both maintenance and spillover hosts can function as vectors in the transmission of disease (Corner *et al.*, 2006). Maintenance hosts, which can spread the infection to other species, are considered true reservoirs of bTB, with implications for disease prevention. *Mycobacterium bovis* transmission occurs via airborne transmission (respiratory droplets) and foodborne transmission (contaminated environment/carcasses).

The interaction of bacterial, host, and environmental factors varies across Europe, creating distinct regional transmission patterns that require tailored management approaches.

The observed transmission patterns exhibit considerable heterogeneity across Europe, delineating three distinct epidemiological scenarios: 1) "Mediterranean hotspots" (Spain/Portugal), where artificial feeding practices sustain wild boar population densities exceeding 30 individuals per

square kilometer (km²), and aerosol transmission is the predominant route (51% pulmonary lesions) (Corner *et al.*, 1981). during periods of summer drought, water scarcity compels atypical aggregations of animals at water sources (Corner *et al.*, 1981). while the implementation of game fencing (Gortázar *et al.*, 2006). contributes to the spatial confinement of pathogens, creating localized transmission foci. In these regions, even scavenging behaviors, particularly the consumption of infected deer offal, are secondary in importance to respiratory dissemination in the propagation of the disease; 2) In contrast, the "Central/Northern ecosystems" (Italy/Germany), characterized by lower wild boar densities (<5 boar/km²), exhibit a shift in the dominant transmission pathway. The prevalence of mandibular lymph node lesions (92.2%) and ileo-cecal involvement indicates that ingestion is the primary route of transmission, facilitated by extensive agricultural practices and the prolonged environmental persistence of the pathogen in moist soil (Bollo *et al.*, 2000; Naranjo *et al.*, 2008; Gortázar *et al.*, 2008; 3). "Transition zones" (France/Alps) display a more complex epidemiological picture. In these areas, fenced regions tend to mimic the patterns observed in Spain (Normandy: 29% prevalence (Palmer *et al.*, 2002), while forested areas show similarities to the trends seen in Italy (Bavaria: 21% PCR + (Müller *et al.*, 2007)).

The epidemiological dynamics in the Alpine region are further complicated by the presence of *Mycobacterium caprae* (Glawischnig *et al.*, 2003) strains, which modify the transmission patterns of bTB.

This complex geographical scenario necessitates region-specific interventions: in areas where aerosol transmission predominates, strategies should focus on banning artificial feeding and implementing respiratory vaccines; in regions where foodborne transmission is the primary route, interventions should include carcass removal and water source protection; and in areas with mixed transmission patterns, combined strategies are required.

These interacting factors—host, pathogen, and environment—are summarized in Fig. (1). which highlights the wild boar (*Sus scrofa*) as a key MTBC reservoir for livestock and humans.

These epidemiological trends highlight three actionable leverage points for targeted intervention strategies:

1. Transmission hotspots: The observed 51%

prevalence of pulmonary lesions in Spanish wild boar populations (Corner *et al.*, 1981) implicates artificial feeding sites as priority targets for mitigation efforts. Conversely, data from Italy, revealing a 92% prevalence of mandibular lesions (Martín-Hernando *et al.*, 2007), suggests that carcass contamination represents the predominant risk factor

2. *super-spreader scenarios*: Juvenile wild boars exhibit a 3.2-fold higher frequency of developing generalized tuberculosis compared to adults, indicating (Martín-Hernando *et al.*, 2007) that targeted removal of infected young animals could proportionally reduce transmission rates
3. Environmental amplification: *Mycobacterium bovis* demonstrates 47% greater persistence in Mediterranean soils compared to Alpine soils, necessitating the implementation of adapted disinfection protocols across different regions

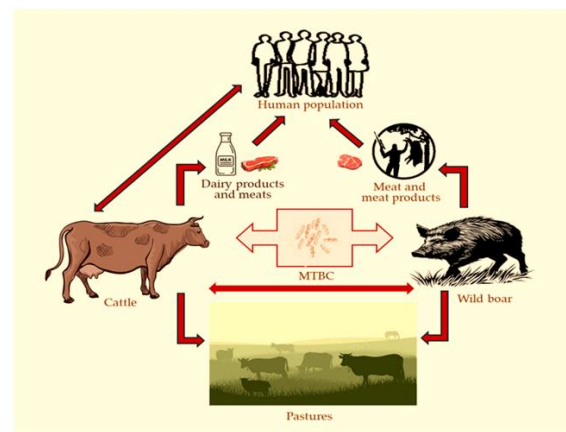


Fig. 1: Transmission dynamics of MTBC, illustrating the role of the European wild boar (*Sus scrofa*) as a reservoir host with implications for both livestock and human populations

Persistence of Disease in Wild Boar Populations

The high prevalence of *Mycobacterium bovis* among wild animal populations is a clear indicator of a self-sustaining, multi-host system of transmission. Within this complex ecological network, the wild boar (*Sus scrofa*) emerges as a central host species, largely due to its behavioral ecology and heightened exposure to infection sources. Wild boars not only serve as key amplifiers of the pathogen but also represent a potential bridge for transmission to both domestic animals and

humans, either directly or indirectly. Infection in wild boars is typically systemic, affecting a wide range of lymphatic and visceral tissues. Lesions characteristic of *Mycobacterium bovis* infection—often considered pathognomonic—are frequently found in lymph nodes associated with both respiratory and digestive tracts, including the retropharyngeal, submandibular, bronchial, mediastinal, hepatic, mammary, subiliac, and popliteal nodes. In addition, the lungs and liver are commonly involved. While these sites are most often affected, pathological involvement of other organs cannot be excluded, reflecting the broad

tissue tropism of the bacterium and the complexity of disease progression in this species (Ciambrone L *et al.*, 2020).

Tuberculosis has been documented in numerous European and non-European countries, underscoring its global significance as a re-emerging zoonotic disease (Barandiaran *et al.*, 2024; Lekko *et al.*, 2021; Brown *et al.*, 2018; Walker *et al.*, 2025). The geographical distribution of *Mycobacterium bovis* (*Mycobacterium bovis*) reservoirs among wild boar populations is summarized in Table 1, highlighting the widespread presence of infected wildlife across different regions.

Table 1: Geographical distribution of *Mycobacterium bovis* in wild boar

Country	Years	Exams and organs	References
Southern Italy (Calabria)	October-dec 2016	Bacterial isolation by PCR, anatomo-pathological lesions	Casalnuovo <i>et al.</i> , 2017
Southern Italy (Campania: Avellino)	March 2019	Bacteriological culture, PCR	Sannino <i>et al.</i> , 2021
Marche	2002-2005	Postmortem specimens: jaw, retropharyngeal nodes, tonsils: LM, WB, hemy-nested-PCR, culturing isolation	Stefano <i>et al.</i> , 2006; Gavaudan <i>et al.</i> , 2019
Northern Italy (Western Liguria)	2000-2016	Anatomopathological examinations	Bona <i>et al.</i> , 2018
Northern Sardinia	2002-2016	Spleen, liver, kidney, intestines, lymph nodes, lungs; PCR	Zanetti <i>et al.</i> , 2008
Central and southern Spain	6 months, not specified year	Lymph nodes from head, neck, thorax and abdomen, bacteriological identification in culture, PCR	Gortazar <i>et al.</i> , 2005
Several sites in Peninsular Spain	1999-2002	Lymph nodes and abdominal and thoracic organs: necropsy: presence of tuberculosis-like lesions	Vicente <i>et al.</i> , 2006
Atlantic Iberian Peninsula	2010-2019	Lymph nodes: cultures and rt-PCR	Varela-Castro <i>et al.</i> , 2021
North-eastern Spain (Catalonia, Valencia, Aragon)	2004-2010	Lymph nodes, serum samples: ELISA	Pérez de Val <i>et al.</i> , 2017
Portugal	2006-2013	Dried blood spots	Santos <i>et al.</i> , 2017
Spain and Portugal (fenced game estates)	2010-2019	Gross pathology, bacteriological culture	Santos <i>et al.</i> , 2022
Iberian Peninsula	2008-2017	Lymph nodes, viscera	Abrantes <i>et al.</i> , 2011
Portugal+Spain (large game)	2017-2022	Meat juice	Abrantes <i>et al.</i> , 2024
California	1961-1967	Serological tests	Walker <i>et al.</i> , 2025
Hawaiian Island of Molokai	1980	Gross lesions	Brown <i>et al.</i> , 2018
USA	2013-2014	Indirect ELISA (only 1 positive)	
Bretonne Forest, Normandy	2005-2006	Retropharyngeal, mediastinic, and mesenteric lymph nodes	Zanella <i>et al.</i> , 2008
France	2013-2017	Submaxillary lymph nodes, PCR, culture on positive PCR pools	Réveillaud <i>et al.</i> , 2018
Slovenia Negative to <i>Mycobacterium bovis</i>	2016-2017	Tissues and blood samples	Pate <i>et al.</i> , 2024
Argentina	2016-2020	Submandibular and mesenteric lymph nodes. PCR, Genotyping	Barandiaran <i>et al.</i> , 2024
Malaysia	2019-2020	Blood samples, tonsils, submandibular, lymph nodes, lungs, tracheobronchial and mediastinic lymph nodes, spleen, liver, kidney, mesenteric LN	Lekko <i>et al.</i> , 2021
Bavaria, southern Germany	1982-1988	Lymph nodes, PCR+, culture -	Müller <i>et al.</i> , 2007
Slovakia, Russia, Bosnia, Herzegovina, Croatia, Hungary, Bulgaria	1983-2000	Faeces, parenchymatous organs	Machackova <i>et al.</i> , 1983

Within Europe, the wild boar (*Sus scrofa*) is increasingly recognized as a key reservoir of *Mycobacterium bovis*, particularly in Mediterranean ecosystems (Santos *et al.*, 2018; Santos *et al.*, 2022; Abrante *et al.*, 2024; 2021; Zanella *et al.*, 2008; Réveillaud *et al.*, 2018; Müller *et al.*, 2013; Machackova *et al.*, 2003; Pate *et al.*, 2024). In southern and central Spain, the economic importance of hunting has transformed land use practices, with many estates relying heavily on revenue from game management. To maximize annual hunting yields, wild boar populations are often intensively managed through practices such as fencing and supplementary feeding. These interventions, while economically beneficial, have inadvertently created conditions conducive to disease persistence and spread. Numerous cases of tuberculosis have been confirmed in Iberian wild boar, providing strong evidence for interspecific transmission within the *Mycobacterium tuberculosis* complex between wild boar and domestic livestock (Varela-Castro *et al.*, 2021).

Beyond animal health implications, these dynamics also raise concerns for human health. Handling of live or deceased infected animals whether during hunting, carcass processing, or fieldwork may pose a zoonotic risk to humans.

In southern Spain, the prevalence of tuberculosis-compatible lesions in wild boars ranges from 46% to 52% (Vicente *et al.*, 2007), a figure that reflects the impact of intensive management practices. Artificial feeding and controlled hunting drive animals into closer contact, thereby maintaining high population densities and significantly amplifying the risk of pathogen transmission (Gortazar *et al.*, 2005; Acevedo *et al.*, 2007). In these high-prevalence zones, respiratory transmission is the dominant route of infection. This is supported by the frequent observation of pulmonary lesions (51%) and thoracic lymph node involvement (52%) (28), patterns that are consistent with aerosol-mediated spread facilitated by aggregation at shared feeding and watering points. Although foodborne transmission also occurs primarily through scavenging of infected carcasses its epidemiological role is considered secondary in these settings (Pérez *et al.*, 2017).

By contrast, the situation in Italy presents a different epidemiological landscape. While prevalence remains notable, it is generally lower than that observed in Spain, ranging from 2.4% in central-northern regions to 8.4% in the south

(Sannino *et al.*, 2021; Bona *et al.*, 2018; Zanetti *et al.*, 2008; Casalnuovo *et al.*, 2017). For instance, data from 2018 indicate that in the Campania region, the incidence of *Mycobacterium bovis* infection among livestock farms ranged from 0.47 to 0.62%, with a mean of 0.53% recorded in Avellino province. In the same region, 10.6% of wild boars tested seropositive for *Mycobacterium bovis* antibodies (Iovane *et al.*, 2020). In the Nebrodi area of southern Italy, a prevalence of 8.4% was reported among wild boars (Di Marco *et al.*, 2012).

In these lower-density ecosystems, foodborne transmission appears to be the predominant infection route. This is reflected in the anatomical distribution of lesions, with 92.2% localized in the mandibular lymph nodes and frequent involvement of the ileocecal valve, suggesting oral exposure via contaminated feed, water, or carcasses (Gortázar *et al.*, 2008; Bollo *et al.*, 2000). Nevertheless, even in these regions, wild boar density remains a critical factor. Aggregation around feeding sites and limited water sources especially during the hot, dry Mediterranean summers facilitates interspecies contact and potential spillover to cattle populations. As such, ecological pressures and land-use practices continue to shape regional transmission patterns, highlighting the need for geographically tailored surveillance and control strategies.

In recent years, the consumption of wild boar meat has extended well beyond the households of hunters, reaching a broader spectrum of consumers and even entering group catering and institutional food services (Clausi *et al.*, 2021). This trend coincides with evolving dietary preferences, which sometimes include the consumption of undercooked or raw game meat—practices that elevate the risk of zoonotic transmission. Although wild boar hunting is regulated by national and regional legislation, and meat consumption is officially permitted only after veterinary inspection, illegal hunting persists in several areas. Such practices facilitate the distribution and consumption of carcasses that have not undergone any sanitary control, increasing the public health risk associated with *Mycobacterium bovis*. The geographical distribution of *Mycobacterium bovis* in wild boar populations across Europe is presented in Table (1).

Wild boars excrete *Mycobacterium bovis* through multiple routes, including faeces, sputum, saliva, and, more rarely, milk. This biological shedding

results in environmental contamination, particularly in areas shared with livestock. On communal pastures, indirect transmission is sustained by faecal contamination and the exchange of excreta, which may contain viable bacilli. In addition, scavenging behavior—especially the ingestion of infected offal—represents a significant transmission risk. Wild boars are particularly susceptible to infection through the consumption of carcasses from tuberculous animals, including deer and other wildlife species (Gortázar *et al.*, 2008).

The wild boar's ecological adaptability, expanding geographical range, and considerable mobility complicate management efforts. Their foraging behavior can lead them to cover distances of up to 80 km per week in search of food resources (Scherer *et al.*, 2019). This high mobility contributes to their role as potential super-spreaders of *Mycobacterium bovis*. Evidence shows that infected individuals can travel between 0 and 20 km from the source of infection to sites of bovine tuberculosis (bTB) outbreaks, with an average distance of 7.38 km recorded between infected wild boars and subsequent cattle infections (Iovane *et al.*, 2020).

From a transmission standpoint, respiratory routes appear to be the most efficient, likely requiring only a minimal infectious dose—as few as five bacilli, comparable to the threshold in cattle. Although *Mycobacterium bovis* can be shed via milk, milk-borne transmission to piglets is considered rare. Likewise, the lack of renal lesions in most infected individuals suggests that urinary excretion is not a major transmission pathway.

The complex interactions among wild boars, cattle, and other wildlife within shared ecosystems highlight the critical need for integrated management strategies aimed at controlling the transmission of bovine tuberculosis (bTB). Effective containment of *Mycobacterium bovis* requires a dual-focus approach that simultaneously addresses wildlife reservoirs and domestic livestock, with tailored interventions based on region-specific transmission dynamics. In regions, where respiratory transmission predominates—such as known transmission hotspots in Mediterranean Spain, where pulmonary lesions are present in 51% of infected wild boars (Corner *et al.*, 1981) artificial feeding stations are recognized as key epidemiological drivers. Management strategies in such contexts should prioritize reduction of population density through the prohibition of supplemental feeding and implementation of oral BCG vaccination to mitigate

aerosol-mediated spread. Conversely, in foodborne-dominant systems—exemplified by rural areas of Italy where mandibular lymph node lesions are found in 92% of infected animals (Martín-Hernando *et al.*, 2020) the principal risk is attributed to oral exposure via contaminated carcasses and water sources. Here, disease control should emphasize carcass removal, biosecure disposal practices, and protection of environmental resources such as water points. Age-related susceptibility also plays a notable role in disease dynamics. Juvenile wild boars develop generalized tuberculosis at a rate 3.2 times higher than adults (Martín-Hernando *et al.*, 2020), indicating that targeted removal of infected juveniles could substantially reduce transmission potential within populations.

Environmental persistence further complicates control efforts. *Mycobacterium bovis* has been shown to survive 47% longer in Mediterranean soils compared to Alpine environments, necessitating the development and application of region-specific decontamination and disinfection protocols. Several universal best practices can be applied across regions to mitigate bTB risk:

- 1) Prohibition of artificial feeding to prevent unnatural aggregation of wild ungulates
- 2) Safe and regulated disposal of hunting remains to limit scavenging-related transmission
- 3) Integrated surveillance systems that monitor both wildlife and livestock populations
- 4) Education of hunters regarding zoonotic risks and biosecurity measures to reduce human-mediated transmission. Artificial feeding not only sustains unnaturally high densities of wild ungulates but also increases contact rates within and between species, thereby amplifying transmission risk. Molecular epidemiological studies have identified several *Mycobacterium bovis* genotypes in wild boars, including SB0120, SB0841, and SB1565. These genotypes reinforce the role of wild boars as key reservoirs and disseminators of *Mycobacterium bovis* across Mediterranean landscapes, underscoring the necessity for holistic, ecosystem-level disease control frameworks

Mycobacterium bovis Persistence in Wildlife Reservoirs

Although cattle remain the principal and most consequential reservoir of *Mycobacterium bovis* and

the dominant source of bovine tuberculosis (bTB) transmission, various wildlife species—beyond wild boars—also function as significant reservoirs and biological vectors of the pathogen. These wild hosts contribute to disease maintenance within sylvatic populations and facilitate spillover events at the wildlife–livestock interface. The identity and epidemiological role of these wildlife reservoirs differ across geographical regions. In South Africa’s Kruger National Park, the African buffalo (*Syncerus caffer*) has been confirmed as a long-term reservoir, capable of transmitting *Mycobacterium bovis* to domestic cattle and thereby sustaining interspecies transmission cycles (De Vos *et al.*, 2022). In North America, particularly in Canada, wood bison (*Bison bison athabasca*) and elk (*Cervus canadensis*) are implicated in the maintenance and propagation of *Mycobacterium bovis* infections across wild and domestic animal populations (Nishi *et al.*, 2006; Andrievskaia *et al.*, 2023). Within Europe, the European badger (*Meles meles*) plays a particularly prominent epidemiological role in countries such as Ireland and the United Kingdom. In these regions, badgers in terminal stages of tuberculosis often display behavioral alterations—including a diminished avoidance of cattle—that increase the likelihood of close contact and promote aerosol-based transmission to livestock (Delahay *et al.*, 2002; Phillips *et al.*, 2003). This modification in behavior associated with advanced infection highlights the intricate nature of interspecies transmission dynamics and emphasizes the need for behavioral ecology to inform disease management strategies.

Cervid species contribute significantly to the transmission and persistence of *Mycobacterium bovis* infections. In Spain, the prevalence of infection in red deer (*Cervus elaphus*) has been reported to reach up to 27%, while fallow deer (*Dama dama*) exhibit infection rates as high as 18% (Vicente *et al.*, 2007). These findings indicate that deer populations—particularly in areas where they are abundant—may function as true reservoir hosts for bovine tuberculosis (bTB) (Gortázar *et al.*, 2008). In New Zealand, the introduced brushtail possum (*Trichosurus vulpecula*) has become a principal wildlife reservoir of *Mycobacterium bovis*. Possums in advanced stages of infection are known to increase their contact with cattle, thereby facilitating interspecies transmission. Similarly, in North America, white-tailed deer (*Odocoileus virginianus*) have emerged as key reservoirs. Their high

population densities—often exacerbated by supplementary feeding and other game management practices—have been linked to elevated rates of aerosol transmission to cattle (Coleman *et al.*, 2001; O’Brien *et al.*, 2006). Wild boars (*Sus scrofa*) represent one of the most prominent wildlife species associated with bTB risk in Europe. They are integral components of several multi-host epidemiological systems, most notably the cattle–deer–wild boar triad (documented in 10 European countries) and the cattle–roe deer–wild boar system (observed in five countries) (Hardstaff *et al.*, 2014). In southern Italy, both wild boars and roe deer (*Capreolus capreolus*) have been identified as primary reservoirs, often harboring *Mycobacterium bovis* strains genetically identical to those found in sympatric cattle herds.

This multifaceted epidemiological landscape highlights the urgent need for comprehensive, integrated control strategies grounded in the One Health framework. Effective management must consider the interplay between wildlife ecology, livestock husbandry, and anthropogenic factors. Since the composition of wildlife reservoirs varies across regions, localized interventions—supported by robust surveillance data and ecological insight—are essential for effective bTB control. Notably, the development and deployment of wildlife vaccination programs, such as the oral BCG vaccine used in badgers in the United Kingdom, represent a promising and sustainable tool for mitigating disease transmission at the wildlife–livestock interface.

Reports of tb Infection in European Wild Animals

Contemporary comprehension of bovine tuberculosis (bTB) dynamics in wildlife populations elucidates intricate interspecies transmission modalities exhibiting marked geographical heterogeneity. The infection, primarily attributable to *Mycobacterium bovis* (*Mycobacterium bovis*), manifests discrete epidemiological profiles across Europe, influenced by host ecology, management protocols, and environmental determinants.

In 2001, a bTB epizootic in the Bretonne Forest unveiled infection rates of 29% in wild boar (*Sus scrofa*) and 13% in red deer (*Cervus elaphus*). Notwithstanding the elevated prevalence in wild boar, lesion distribution topographies implied red deer as the principal maintenance host, with subsequent spillover into wild boar populations. This ascertainment precipitated the implementation of containment strategies, encompassing the

construction of wildlife-impermeable fencing, obligatory disposal of slaughter by-products, and selective culling of red deer populations.

Of particular note, molecular epidemiological inquiries discerned identical *Mycobacterium bovis* genotypes circulating in sympatric cattle, domestic pigs, and wild boar populations, whereas deer isolates manifested disparate strain profiles. This genetic corroboration bolsters the postulation of independent transmission cycles in cattle-boar and deer populations.

In Italy, surveillance data from 2007 identified *Mycobacterium bovis* infection in 217 of 3,166 examined wild boar (6.8% prevalence) (EFSA, 2007). Regional investigations in Sicily demonstrated 9.4% PCR positivity in mandibular lymph nodes of free-ranging domestic pigs (Di Marco *et al.*, 2008), while in Sardinia wild suids presented PCR-positive but culture-negative finding (Zanetti *et al.*, 2008). Cervid species demonstrated minimal involvement, with documented cases limited to imported red deer populations and a single instance in Aosta Valley (Balseiro *et al.*, 2009).

Contemporary investigations into prevalence, conducted in 2018, have delineated geographical variability in infection rates among wild boar populations, with observed rates fluctuating from 2.4% in the central and northern regions of Italy to 8.4% in the southern regions (Sannino *et al.*, 2021). The Benelux countries exhibit a discrete epidemiological context. Risk evaluations performed in Belgium concerning sporadic bTB outbreaks have not yielded substantiation of wildlife reservoir participation. Nevertheless, potential epidemiological confluences with France and the United Kingdom have mandated continued wildlife surveillance efforts (Humblot *et al.*, 2010).

The Scandinavian countries, encompassing Sweden, Denmark, Finland, and Norway, uphold Officially Tuberculosis-Free status in their domestic cattle populations. This status is maintained despite the absence of reported cases in wildlife, a condition achieved through the implementation of comprehensive monitoring systems (Bölske *et al.*, 1995). Historical anomalies include: 1) the occurrence of tuberculosis outbreaks within Swedish captive cervid populations in 1991, and 2) the subsequent tracing of all identified cases to animals imported from the United Kingdom in 1987 (Bölske *et al.*, 1995).

Surveillance efforts in Germany have revealed

multifaceted patterns of transmission. During the period 1982–1988, a prevalence of tuberculous lesions was identified in 1.4% of wild boar examined ($n = 7,419$), with 0.8% of individuals yielding culture-positive results for *Mycobacterium bovis*. Additionally, molecular diagnostics applied to lymph node samples from Bavaria ($n = 92$) demonstrated a 21% positivity rate for Mycobacterium Tuberculosis Complex (MTBC) DNA (Schulz *et al.*, 1992).

In the Alpine ecosystem, *M. caprae* exhibits a distinct epidemiological behavior. Evidence suggests (Barroso *et al.*, 2023). persistent maintenance within free-ranging red deer populations; (Gortazar *et al.*, 2005). isolation of the pathogen from seven infected animals in the Northern Austrian Alps (Glawischnig *et al.*, 2003; Neill *et al.*, 2005). cross-species transmission affecting domesticated livestock in adjacent areas. Data from Eastern Europe, as compiled by Machackova *et al.* (2003). document longitudinal trends between 1983 and 2000, indicating a 20% infection rate in wild boar populations in Slovakia (46 individuals), approximately 5% prevalence in various wildlife species across the Russian Federation, and geographically constrained outbreaks reported in Bosnia and Herzegovina, Croatia, Hungary, and Bulgaria.

Host-specific insights further highlight the zoonotic and ecological relevance of MTBC: thirteen infections in European bison (*Bison bonasus*) in Poland (Bölske *et al.*, 2005). documented occurrences in roe deer from Poland ($n = 2$) and Hungary; and multiple *M. caprae* strains isolated from wildlife in Hungary (Lipiec *et al.*, 2018; Erler *et al.*, 2004).

Understanding the Burden of Tuberculosis in the Wild Boar: An Examination of Infection Sites and Clinical Features

A thorough understanding of infection dynamics particularly the anatomical distribution and severity of lesions is essential for implementing effective strategies for disease surveillance and control. A pivotal investigation by Martín-Hernando *et al.* (2007). involving 127 Mycobacterium Tuberculosis

Complex (MTBC)-positive European wild boar, reported a high occurrence of visible lesions (82.7%), while a smaller subset (8.7%) exhibited only histologically detectable microscopic changes. These findings underscored the pervasive nature of

the disease, with 57.8% of individuals displaying disseminated tuberculosis and 42.2% showing localized pathology.

Mandibular LNs emerged as the most consistently affected anatomical site, with involvement observed in 92.2% of subjects corroborating prior studies that designate LNs as primary sentinel tissues for TB detection in wild boar (Bollo *et al.*, 2000a-b; Gortazar *et al.*, 2003). Additionally, pulmonary lesions were prominent, with 51% of animals presenting infection in either the lung parenchyma or thoracic LNs (Corner *et al.*, 1981). Granuloma morphology varied according to disease stage: localized infections were characterized by mixed inflammatory infiltrates, while advanced cases displayed necrotic and mineralized granulomas (Martín-Hernando *et al.*, 2007).

Juvenile wild boar frequently exhibited lesions in multiple organ systems, with the lungs commonly representing the primary site of infection. This pattern aligns with observations from a 2019 case report in Southern Italy (Sannino *et al.*, 2021), reinforcing the age-related vulnerability to systemic disease spread. The study conducted in Mediterranean Spain where anthropogenic factors such as fencing and supplementary feeding have led to elevated wild boar densities provides compelling evidence, supported by molecular and field epidemiological data, that wild boar may function as true maintenance hosts for TB in this region.

Histological examination was instrumental in detecting lesions in the ileocecal valve, lungs (38%), and tonsils (44%), highlighting the diagnostic value of tissue-based methods in tuberculosis research. Concurrent detection of lesions in all three major cranial lymph nodes (mandibular, medial retropharyngeal, and parotid), along with tonsillar involvement, suggested systemic disease affecting multiple head regions an observation of particular relevance to post-mortem meat inspection. Notably, this investigation revealed a predominance of calcified granulomas over necrotic or mixed necrotic-calcified types, a distribution that contrasts with previous literature (Martín-Hernando *et al.*, 2007).

Comparative insights from studies on feral pig populations in other geographic regions further contextualize these findings. In Australia, research has indicated that feral pigs exhibit a low prevalence of systemic TB, with no significant pulmonary involvement or evidence of pathogen excretion features that position them more likely as dead-end

hosts. This notion is reinforced by the rapid decline in TB prevalence following the eradication of the disease in local cattle herds (Corner, 2006).

Conversely, TB dynamics in New Zealand's feral pig populations display substantial heterogeneity, with prevalence rates reaching up to 96% in certain regions. Reports of widespread, generalized infection in 63% of examined pigs suggest early-life exposure and rapid disease progression (Co DO, 2004).

Age-stratified analyses of granuloma types in wild boar populations have demonstrated a uniform distribution of lesion stages, including calcified forms even in younger individuals. Although generalized TB was detected across all age groups, extensive lesions (type B) were disproportionately frequent among juveniles. This pattern may indicate increased mortality rates in younger boar and could partially account for the age-specific lesion distribution. In contrast, adult individuals may exhibit enhanced immunological control over infection, potentially allowing partial resolution of disease.

Zoonotic Transmission and Diagnostic Challenges

While human tuberculosis caused by *M. tuberculosis* remains a leading cause of infectious disease death globally, the contribution of animal mycobacteria to human disease represents an underestimated but significant component of the overall disease burden. Zoonotic tuberculosis, mainly caused by *Mycobacterium bovis*, complicates the clinical and epidemiological picture of human TB, with important implications for diagnosis and treatment. The difficulty in distinguishing *Mycobacterium bovis* from *M. tuberculosis* in routine diagnostic tests and its intrinsic resistance to pyrazinamide complicate clinical management and likely contribute to the underestimation of its impact (Olea-Popelka *et al.*, 2017).

Regional studies reveal varying prevalence rates: in endemic areas, according to certain investigations, the isolation rate of *Mycobacterium bovis* from human patients exhibiting symptoms was 6.9% in Uganda and 13.8% in Mexico (Pérez-Guerrero *et al.*, 2008). 5% in Nigeria (Cadmus *et al.*, 2006) 0.5% in Taiwan (Jou *et al.*, 2008), and 0–2.5% in ten Latin American nations (De Kantor *et al.*, 2008; Oloya *et al.*, 2008).

However, among high-risk populations this proportion can rise substantially, underscoring a significant yet often overlooked public health impact (Ben Ayed *et al.*, 2018; Dong *et al.*, 2022).

These data highlight the geographic variability of zoonotic TB and emphasize the need for improved surveillance systems and diagnostic capabilities, particularly in high-burden regions where the intersection of human and animal health creates unique challenges for tuberculosis control efforts.

According to the 2020 World Health Organization (WHO) Global Tuberculosis Report, 10 million persons (range: 8.9–11.0 million) contracted TB disease in 2019, of whom 1.2 million died. The TB-HIV syndemic was also responsible for an additional 208,000 deaths (World Health Organization, 2020).

The documented incidence of zoonotic tuberculosis (zTB) is rather modest, despite the fact that South Asia has the largest burden of TB, which may be connected to high rates of poverty, rapid urbanization, high population density, greater prevalence of diabetes, and high air pollution (Basnyat *et al.*, 2020).

Though *M. orygis* appears to be the main pathogen in Indian cattle, *Bos indicus*, this might be partially explained by inadequate laboratory facilities and a lack of precise identification of the zTB causal agent (Brites *et al.*, 2018). The use of unpasteurized milk and milk products, close and frequent physical contact with infected animals, high human-animal density, and insufficient disease management methods are some of the region's many risk factors for zTB (Bapat *et al.*, 2017).

For instance, in India's rapidly expanding dairy industry, there are an estimated 21.8 million (95% CI: 16.6, 28.4) infected cattle (Srinivasan *et al.*, 2018). On the other hand, the European region has one of the lowest rates of tuberculosis (TB) in the world (World Health Organization, 2014)). It has been steadily declining since 2015 and currently stands at 10 cases per 100,000 people, with the incidence being unevenly distributed within the European Union and European Economic Area. The majority of zTB cases in this region are caused by *Mycobacterium bovis* and *Mycobacterium caprae*, and their percentage of TB cases is less than 0.01% (Müller *et al.*, 2013). This stark contrast between regions illustrates how socioeconomic factors, agricultural practices, and healthcare infrastructure significantly influence zTB prevalence and control.

Previous experiences highlight regions where living circumstances encourage close contact with diseased animals, which might lead to the spread of aerosols, or where unpasteurized milk products (like

queso fresco) are consumed. In addition to non-milk-producing animals like rodents (*M. microti*), banded mongooses (*M. mungi*), seals, and sea lions (*M. pinnipedii*), there are infrequent transmission events from sheep and goats that are caused by *M. caprae*. Additionally, there are growing reports of *M. orygis* from Indian cattle (Duffy *et al.*, 2020; Brites *et al.*, 2018; Jagielski *et al.*, 2016).

The health of cattle and other animal species is also negatively impacted by various MTBC species, which has an effect on livelihoods, animal-based industrial food systems, and wildlife conservation. These include many iconic species like bison, rhinos, lions, and even the critically endangered African wild dog (Marais *et al.*, 2019; Sichewo *et al.*, 2019; De Garine-Wichatitsky *et al.*, 2013). In addition to the main reservoir cattle, the presence of zTB animal carriers exacerbates the issue with species such as deer, buffalo, European badgers, wild boar, brushtail possums, bison, goats, camelids (including alpaca, llama, and camels), pigs, antelopes, dogs, and cats. However, even among species that are highly prevalent, such European badgers and African buffalo, the incidence and/or danger of MTBC species being transmitted from free-living wildlife to people is still quite low (Biet *et al.*, 2005). This complex interspecies transmission landscape demonstrates that zoonotic TB represents not just a public health challenge, but also a significant One Health issue requiring collaborative approaches across human, animal, and environmental health sectors.

Some risk factor surveys have investigated the relationship between cattle TB prevalence and interacting with wildlife, and some (Sichewo *et al.*, 2019) predict that the prevalence of TB in cattle is higher in scenarios involving severe co-grazing and sharing of water resources in the USA and Africa. Uncertainties surround this issue, though, as the power of infection in these trials and other cases mentioned is not certain. For instance, TB investigations conducted in the UK raise concerns about the directionality and rate of transmission between cattle and badgers (Sandoval Barron *et al.*, 2018). According to (Meunier *et al.*, 2017; Meunier *et al.*, 2017), rare research of this interface in a mixed system in Uganda revealed that infection prevalence rates in wild buffalo were 10 times greater than in co-grazing cattle, indicating a low rate of transmission from wildlife to cattle. These findings highlight the complexity of wildlife-livestock-human transmission dynamics and emphasize the

need for context-specific research and interventions. Despite extensive research, significant knowledge gaps remain regarding transmission routes, species-specific susceptibility, and effective control measures across different ecological settings. Addressing zoonotic tuberculosis effectively will require integrated surveillance systems, improved diagnostic capabilities, and tailored control strategies that account for regional variations in host species, environmental factors, and human behaviors.

In most cases, disease prevention represents the sole approach by which to ensure the health status of natural populations. Studies unraveling the wild boar genetic mechanisms involved in susceptibility to TB would be necessary too. They may lead to a better understanding of TB pathogenesis by identifying loci associated with genetic susceptibility to tuberculosis in wild boar facilitating the development of new strategies for the prevention and treatment of TB in humans and animals (Queirós *et al.*, 2018).

The growing body of evidence underscores the significant role of diverse wildlife species in the epidemiology of *Mycobacterium bovis*, revealing the complexity of managing bovine tuberculosis across both domestic and wildlife populations. Given the varied geographic distribution and taxonomic range of affected species, a comprehensive approach to disease monitoring and management is essential to mitigate further cross-species transmission.

Conclusion

bTB remains a pressing global challenge for both veterinary and human health systems. Despite notable progress in disease containment across certain territories, eradication efforts continue to face setbacks due to the enduring presence of infection in wildlife hosts—chief among them the European wild boar (*Sus scrofa*), which serves as a pivotal reservoir species that sustains and propagates the pathogen.

Epidemiological patterns of bTB across the European continent are highly heterogeneous. Regions such as southern Italy and Spain consistently report elevated infection rates, contrasting sharply with lower prevalence zones in northern and central Europe. This spatial variability arises from an interplay of contributing factors, including intensive animal husbandry practices, frequent contact between wildlife and livestock, and ecological conditions favorable to

the persistence and transmission of *Mycobacterium bovis*.

In particular, the European wild boar plays an instrumental role in the maintenance and dissemination of *Mycobacterium bovis*, especially in southwestern Europe, where dense populations of wild ungulates act as long-term reservoirs. In Spain, for example, wild boar—often in conjunction with red deer—are integral to the sylvatic transmission cycle, maintaining infection pressure on both wildlife and domestic animal populations. The potential for cross-species transmission is significantly amplified in shared landscapes, where wild boar and livestock utilize overlapping pastures, water points, and feeding areas, creating a high-risk interface for disease spillover.

These multifaceted transmission dynamics present serious obstacles for bTB control and emphasize the zoonotic risk posed by environmental exposure, especially in endemic zones. As such, a comprehensive and integrative disease management framework is essential. This should align with the One Health paradigm, addressing the interdependencies between environmental, animal, and human health domains.

A strategic response must include enhanced diagnostic surveillance across domestic and wildlife populations, targeted immunization campaigns, and strict biosecurity measures to curb interspecies transmission. In regions with robust wild boar populations, wildlife-focused interventions become critical. These may encompass population control (e.g., selective culling), oral vaccination initiatives, or habitat management aimed at reducing boar-livestock interactions.

The persistent role of wild boar as a primary reservoir of *Mycobacterium bovis* underscores the urgent need for further ecological and epidemiological research. Investigations into host-pathogen-environment dynamics, interspecies contact networks, and land-use practices are vital for refining mitigation strategies. Furthermore, innovation in wildlife vaccination technologies and the development of sensitive, field-adaptable diagnostic assays will be essential for achieving more effective control of bTB in endemic wildlife-livestock ecosystems.

Funding Information

This research received no external funding.

Author's Contributions

Giovanna Liguori: Conceptualization, methodology, literature search, screening and eligibility assessment, data extraction, data curation, draft preparation, coordination of data analysis, supervision, final approval of the manuscript.

Renato Lombardi: Conceptualization, study design and organization, literature search, screening and eligibility assessment, data extraction, draft preparation, final approval of the manuscript.

Fabio Castagna: Study design and organization, literature search, screening and eligibility assessment, data extraction, draft preparation, final approval of the manuscript.

Roberto Bava: Data analysis coordination, writing review and editing, literature search, screening and eligibility assessment, data extraction, final approval of the manuscript.

Nadia Piscopo: Massimiliano Quintiliani, Margherita D'Angelo, Grazia Matarante, Anna Costagliola, Ernesto Palma and Domenico Britti: Literature search, screening and eligibility assessment, data extraction, draft preparation, final approval of the manuscript.

Antonio Giordano: Supervision, critical review of the draft manuscript, literature search, screening and eligibility assessment, data extraction, draft preparation, final approval of the manuscript.

Ethics

This study is a literature review and did not involve direct experimentation on animals or wildlife.

Conflicts of Interest

The authors declare no conflicts of interest.

References

- Abrantes, A. C., Risco, D., Carvalho, M., Cerrato, R., Fernández-Llario, P., & Vieira-Pinto, M. (2024). Meat juice as a feasible alternative sample for tuberculosis surveillance in large game. *Veterinaria Italiana*, 60(1), 43–50. <https://doi.org/10.12834/VetIt.3132.22735.2>
- Abrantes, A. C., Serejo, J., & Vieira-Pinto, M. (2021). The Association between Palmer Drought Severity Index Data and Tuberculosis-like Lesions Occurrence in Mediterranean Hunted Wild Boars. *Animals*, 11(7), 2060. <https://doi.org/10.3390/ani11072060>
- Acevedo, P., Vicente, J., Höfle, U., Cassinello, J., Ruiz-Fons, F., & Gortázar, C. (2007). Estimation of European wild boar relative abundance and aggregation: a novel method in epidemiological risk assessment. *Epidemiology and Infection*, 135(3), 519–527. <https://doi.org/10.1017/s0950268806007059>
- Amanfu, W. (2006). The situation of tuberculosis and tuberculosis control in animals of economic interest. *Tuberculosis*, 86(3–4), 330–335. <https://doi.org/10.1016/j.tube.2006.01.007>
- Andrievskaia, O., Garceac, A., Lloyd, D., Savic, M., & Duceppe, M.-O. (2023). Complete Genome Sequences of Mycobacterium bovis Strains Affiliated with Bovine Tuberculosis Outbreaks in Canada in 2016 and 2018. *Microbiology Resource Announcements*, 12(3), e01213–e01222. <https://doi.org/10.1128/mra.01213-22>
- Aranaz, A., de Juan, L., Montero, N., Sánchez, C., Galka, M., Delso, C., Álvarez, J., Romero, B., Bezos, J., Vela, A. I., Briones, V., Mateos, A., & Domínguez, L. (2004). Bovine Tuberculosis (Mycobacterium bovis) in Wildlife in Spain. *Journal of Clinical Microbiology*, 42(6), 2602–2608. <https://doi.org/10.1128/jcm.42.6.2602-2608.2004>
- Aranaz, A., Liébana, E., Mateos, A., Domínguez, L., Vidal, D., Domingo, M., Gonzolez, O., Rodriguez-Ferri, E. F., Bunschoten, A. E., Van Embden, J. D., & Cousins, D. (1996). Spacer oligonucleotide typing of Mycobacterium bovis strains from cattle and other animals: a tool for studying epidemiology of tuberculosis. *Journal of Clinical Microbiology*, 34(11), 2734–2740. <https://doi.org/10.1128/jcm.34.11.2734-2740.1996>
- Balseiro, A., Oleaga, A., Orusa, R., Robetto, S., Domenis, L., Zoppi, S., Dondo, A., Gorla, M., Gortázar, C., & García Marín, J. F. (2009). Tuberculosis in roe deer from Spain and Italy. *Veterinary Record*, 164(15), 468–470. <https://doi.org/10.1136/vr.164.15.468>
- Bapat, P. R., Dodkey, R. S., Shekhawat, S. D., Husain, A. A., Nayak, A. R., Kawle, A. P., Daginawala, H. F., Singh, L. K., & Kashyap, R. S. (2017). Prevalence of zoonotic tuberculosis and associated risk factors in Central Indian populations. *Journal of Epidemiology and Global Health*, 7(4), 277. <https://doi.org/10.1016/j.jegh.2017.08.007>
- Barandiaran, S., Marfil, M. J., La Sala, L. F., Tammone, A., Condori, W. E., Winter, M., Abate, S., Rosas, A. C., Ponce, L., Carpinetti, B., Serena, M. S., Lozano Calderón, L. C., & Zumárraga, M. J. (2024). Tuberculosis in Wild Pigs from Argentina. *EcoHealth*, 21(1), 71–82. <https://doi.org/10.1007/s10393-024-01681-y>
- Barroso, P., Serrano, E., Carpio, A. J., Acevedo, P., Vicente, J., & Gortázar, C. (2023). Low impact of tuberculosis severity on wild boar body condition. *Research in Veterinary Science*, 155, 161–167. <https://doi.org/10.1016/j.rvsc.2023.01.014>
- Basnyat, B., Caws, M., & Udawadia, Z. (2018). Tuberculosis in South Asia: a tide in the affairs of men. *Multidisciplinary Respiratory Medicine*, 13(1), 10. <https://doi.org/10.1186/s40248-018-0122-y>

- Biet, F., Boschirol, M. L., Thorel, M. F., & Guilloteau, L. A. (2005). Zoonotic aspects of *ycobacterium bovis* and *Mycobacterium avium-intracellulare* complex (MAC). *Veterinary Research*, 36(3), 411–436.
<https://doi.org/10.1051/vetres:2005001>
- Bollo, E., Ferroglio, E., Dini, V., Mignone, W., Biollatti, B., & Rossi, L. (2000). Detection of *Mycobacterium tuberculosis* Complex in Lymph Nodes of Wild Boar (*Sus scrofa*) by a Target-Amplified Test System. *Journal of Veterinary Medicine, Series B*, 47(5), 337–342.
<https://doi.org/10.1046/j.1439-0450.2000.00354.x>
- Bollo, E., Ferroglio, E., Dini, V., Mignone, W., Biollatti, B., & Rossi, L. (2000). Detection of *Mycobacterium tuberculosis* Complex in Lymph Nodes of Wild Boar (*Sus scrofa*) by a Target-Amplified Test System. *Journal of Veterinary Medicine, Series B*, 47(5), 337–342.
<https://doi.org/10.1046/j.1439-0450.2000.00354.x>
- Bolske, G., Englund, L., Wahlstrom, H., de Lisle, G., Collins, D., & Croston, P. (1995). Bovine tuberculosis in Swedish deer farms: epidemiological investigations and tracing using restriction fragment analysis. *Veterinary Record*, 136(16), 414–417.
<https://doi.org/10.1136/vr.136.16.414>
- Bona, M. C., Mignone, W., Ballardini, M., Dondo, A., Mignone, G., & Ru, G. (2018). Tuberculosis in wild boar (*Sus scrofa*) in the Western Liguria Region. *Épidémiologie Et St. Anim*, 74, 151–158.
- Brites, D., Loiseau, C., Menardo, F., Borrell, S., Boniotti, M. B., Warren, R., Dippenaar, A., Parsons, S. D. C., Beisel, C., Behr, M. A., Fyfe, J. A., Coscolla, M., & Gagneux, S. (2018). A New Phylogenetic Framework for the Animal-Adapted *Mycobacterium tuberculosis* Complex. *Frontiers in Microbiology*, 9, 2820.
<https://doi.org/10.3389/fmicb.2018.02820>
- Brites, D., Loiseau, C., Menardo, F., Borrell, S., Boniotti, M. B., Warren, R., Dippenaar, A., Parsons, S. D. C., Beisel, C., Behr, M. A., Fyfe, J. A., Coscolla, M., & Gagneux, S. (2018). A New Phylogenetic Framework for the Animal-Adapted *Mycobacterium tuberculosis* Complex. *Frontiers in Microbiology*, 9, 2820.
<https://doi.org/10.3389/fmicb.2018.02820>
- Brown, V. R., Bowen, R. A., & Bosco-Lauth, A. M. (2018). Zoonotic pathogens from feral swine that pose a significant threat to public health. *Transboundary and Emerging Diseases*, 65(3), 649–659. <https://doi.org/10.1111/tbed.12820>
- Cadmus, S., Palmer, S., Okker, M., Dale, J., Gover, K., Smith, N., Jahans, K., Hewinson, R. G., & Gordon, S. V. (2006). Molecular Analysis of Human and Bovine Tubercle Bacilli from a Local Setting in Nigeria. *Journal of Clinical Microbiology*, 44(1), 29–34. <https://doi.org/10.1128/jcm.44.1.29-34.2006>
- Casalinuovo, F., Ciabrone, L., Grillone, R., & De Gori, N. (2017). Tuberculosis in wild boar and the risk of human infection by *Mycobacterium bovis* results of a study conducted in Southern Italy. *J Food Microbiol*, 1(1), 22–26.
- Ciabrone, L., Gioffrè, A., Musarella, R., Samele, P., Visaggio, D., Pirolo, M., Clausi, M. T., Di Natale, R., Gherardi, M., Spatari, G., Visca, P., & Casalinuovo, F. (2020). Presence of *Mycobacterium bovis* in slaughterhouses and risks for workers. *Preventive Veterinary Medicine*, 181, 105072.
<https://doi.org/10.1016/j.prevetmed.2020.105072>
- Clausi, M. T., Ciabrone, L., Zanoni, M., Costanzo, N., Pacciarini, M., & Casalinuovo, F. (2021). Evaluation of the Presence and Viability of *Mycobacterium bovis* in Wild Boar Meat and Meat-Based Preparations. *Foods*, 10(10), 2410.
<https://doi.org/10.3390/foods10102410>
- Co, D. O., Hogan, L. H., Kim, S.-I., & Sandor, M. (2004). *Mycobacterial* granulomas: keys to a long-lasting host–pathogen relationship. *Clinical Immunology*, 113(2), 130–136. <https://doi.org/10.1016/j.clim.2004.08.012>
- Coleman, J. D., & Cooke, M. M. (2001). *Mycobacterium bovis* infection in wildlife in New Zealand. *Tuberculosis*, 81(3), 191–202.
<https://doi.org/10.1054/tube.2001.0291>
- Corner, L. A. L. (2006). The role of wild animal populations in the epidemiology of tuberculosis in domestic animals: How to assess the risk. *Veterinary Microbiology*, 112(2–4), 303–312.
<https://doi.org/10.1016/j.vetmic.2005.11.015>
- Corner, L. A., Barrett, R. H., Lepper, A. W. D., Lewis, V., & Pearson, C. W. (1981). A survey of mycobacteriosis of feral pigs in the northern territory. *Australian Veterinary Journal*, 57(12), 537–542. <https://doi.org/10.1111/j.1751-0813.1981.tb00428.x>
- Cousins, D. V. (2001). *Mycobacterium bovis* infection and control in domestic livestock. *Revue Scientifique et Technique de l'OIE*, 20(1), 71–85.
<https://doi.org/10.20506/rst.20.1.1263>
- De Garine-Wichatitsky, M., Caron, A., Kocka, R., Tschopp, R., Munyeme, M., Hofmeyr, M., & Michel, A. (2013). A review of bovine tuberculosis at the wildlife–livestock–human interface in sub-Saharan Africa. *Epidemiology and Infection*, 141(7), 1342–1356. <https://doi.org/10.1017/s0950268813000708>
- de Kantor, I. N., Ambroggi, M., Poggi, S., Morcillo, N., Da Silva Telles, M. A., Osório Ribeiro, M., Garzón Torres, M. C., Llerena Polo, C., Ribón, W., García, V., Kuffo, D., Asencios, L., Vázquez Campos, L. M., Rivas, C., & de Waard, J. H. (2008). Human *Mycobacterium bovis* infection in ten Latin American countries. *Tuberculosis*, 88(4), 358–365.
<https://doi.org/10.1016/j.tube.2007.11.007>

- De Vos, V., Bengis, R. G., Kriek, N. P. J., Keet, D. F., Raath, J. P., Huchzermeyer, H. F., & Michel, A. L. (2022). The Epidemiology of Tuberculosis in Free-Ranging African Buffalo (*Syncerus caffer*) in the Kruger National Park, South Africa. *Proceedings of the National Academy of Sciences of the United States of America (PNAS)*, 119(24), e2120656119. <https://doi.org/10.1073/pnas.2120656119>
- Delahay, R. J., De Leeuw, A. N. S., Barlow, A. M., Clifton-Hadley, R. S., & Cheeseman, C. L. (2002). The Status of *Mycobacterium bovis* Infection in UK Wild Mammals: A Review. *The Veterinary Journal*, 164(2), 90–105. <https://doi.org/10.1053/tvjl.2001.0667>
- Di Marco, V., Mazzone, P., Capucchio, M. T., Boniotti, M. B., Aronica, V., Russo, M., Fiasconaro, M., Cifani, N., Corneli, S., Biasibetti, E., Biagetti, M., Pacciarini, M. L., Cagiola, M., Pasquali, P., & Marianelli, C. (2012). Epidemiological Significance of the Domestic Black Pig (*Sus scrofa*) in Maintenance of Bovine Tuberculosis in Sicily. *Journal of Clinical Microbiology*, 50(4), 1209–1218. <https://doi.org/10.1128/jcm.06544-11>
- Dong, Z., Wang, Q.-Q., Yu, S.-C., Huang, F., Liu, J.-J., Yao, H.-Y., & Zhao, Y.-L. (2022). Age–period–cohort analysis of pulmonary tuberculosis reported incidence, China, 2006–2020. *Infectious Diseases of Poverty*, 11(1), 85. <https://doi.org/10.1186/s40249-022-01009-4>
- Duffy, S. C., Srinivasan, S., Schilling, M. A., Stuber, T., Danchuk, S. N., Michael, J. S., Venkatesan, M., Bansal, N., Maan, S., Jindal, N., Chaudhary, D., Dandapat, P., Katani, R., Chothe, S., Veerasami, M., Robbe-Austerman, S., Juleff, N., Kapur, V., & Behr, M. A. (2020). Reconsidering *Mycobacterium bovis* as a proxy for zoonotic tuberculosis: a molecular epidemiological surveillance study. *The Lancet Microbe*, 1(2), e66–e73. [https://doi.org/10.1016/s2666-5247\(20\)30038-0](https://doi.org/10.1016/s2666-5247(20)30038-0)
- Erler, W., Martin, G., Sachse, K., Naumann, L., Kahlau, D., Beer, J., Bartos, M., Nagy, G., Cvetnic, Z., Zolnir-Dovc, M., & Pavlik, I. (2004). Molecular Fingerprinting of *Mycobacterium bovis* subsp. *Caprae* Isolates from Central Europe. *Journal of Clinical Microbiology*, 42(5), 2234–2238. <https://doi.org/10.1128/jcm.42.5.2234-2238.2004>
- European Food Safety Authority (EFSA). (2009). The Community Summary Report on Trends and Sources of Zoonoses and Zoonotic Agents in the European Union in 2007. *EFSA Journal*, 7(1), 223r. <https://doi.org/10.2903/j.efsa.2009.223r>
- European Food Safety Authority and European Centre for Disease Prevention and Control (EFSA and ECDC), E. (2018). The European Union summary report on trends and sources of zoonoses, zoonotic agents and food-borne outbreaks in 2017. *EFSA Journal*, 16(12), e05500. <https://doi.org/10.2903/j.efsa.2018.5500>
- Gavaudan, S., Conquista, M., Barchiesi, F., Canonico, C., Angeloni, G., Perugini, G., Aconiti Mandolini, N., P.Papa, P., Crotti, S., Mazzone, P., Gaspari, M., & Barboni, C. (2019). Morandi F. Sorveglianza della tubercolosi bovina nel cinghiale. *Osservazioni epidemiologiche*, 201–208.
- Glawischnig, W., Allerberger, F., Messner, C., Schönbauer, M., & Prodinger, W. M. (2003). Tuberculosis in Free-Living Red Deer (*Cervus Elaphus Hippelaphus*) in the Northern Alps. *Wiener Tierärztliche Monatsschrift*, 90(2), 38–44.
- Gortázar, C., Acevedo, P., Ruiz-Fons, F., & Vicente, J. (2006). Disease risks and overabundance of game species. *European Journal of Wildlife Research*, 52(2), 81–87. <https://doi.org/10.1007/s10344-005-0022-2>
- Gortázar, C., Torres, M. J., Vicente, J., Acevedo, P., Reglero, M., de la Fuente, J., Negro, J. J., & Aznar-Martín, J. (2008). Bovine Tuberculosis in Doñana Biosphere Reserve: The Role of Wild Ungulates as Disease Reservoirs in the Last Iberian Lynx Strongholds. *PLoS ONE*, 3(7), e2776. <https://doi.org/10.1371/journal.pone.0002776>
- Gortazar, C., Vicente, J., & Gavier-Widén, D. (2003). Pathology of bovine tuberculosis in the European wild boar (*Sus scrofa*). *Veterinary Record*, 152(25), 779–780. <https://doi.org/10.1136/vr.152.25.779>
- Gortazar, C., Vicente, Joaquín, Samper, S., Garrido, J. M., Fernández-De-Mera, I. G., Gavín, P., Juste, Ramón A, Martín, C., Acevedo, P., De La Puente, M., & Höflea, U. (2005). Molecular characterization of *Mycobacterium tuberculosis* complex isolates from wild ungulates in south-central Spain. *Veterinary Research*, 36(1), 43–52. <https://doi.org/10.1051/vetres:2004051>
- Hardstaff, J. L., Marion, G., Hutchings, M. R., & White, P. C. L. (2014). Evaluating the tuberculosis hazard posed to cattle from wildlife across Europe. *Research in Veterinary Science*, 97, S86–S93. <https://doi.org/10.1016/j.rvsc.2013.12.002>
- Humblet, M.-F., Gilbert, M., Govaerts, M., Fauville-Dufaux, M., Walravens, K., & Saegerman, C. (2010). New Assessment of Bovine Tuberculosis Risk Factors in Belgium Based on Nationwide Molecular Epidemiology. *Journal of Clinical Microbiology*, 48(8), 2802–2808. <https://doi.org/10.1128/jcm.00293-10>
- Humphrey, H. M., Orloski, K. A., & Olea-Popelka, F. J. (2014). Bovine tuberculosis slaughter surveillance in the United States 2001–2010: assessment of its traceback investigation function. *BMC Veterinary Research*, 10(1), 182. <https://doi.org/10.1186/s12917-014-0182-y>

- Iovane, V., Ferrara, G., Petrucci, A., Veneziano, V., D'Alessio, N., Ciarcia, R., Fioretti, A., Pagnini, U., & Montagnaro, S. (2020). Prevalence of serum antibodies against the Mycobacterium tuberculosis complex in wild boar in Campania region, Italy. *European Journal of Wildlife Research*, 66(1), 6. <https://doi.org/10.1007/s10344-019-1359-2>
- Jagielski, T., Minias, A., van Ingen, J., Rastogi, N., Brzostek, A., Żaczek, A., & Dziadek, J. (2016). Methodological and Clinical Aspects of the Molecular Epidemiology of Mycobacterium tuberculosis and Other Mycobacteria. *Clinical Microbiology Reviews*, 29(2), 239–290. <https://doi.org/10.1128/cmr.00055-15>
- Jou, R., Huang, W.-L., & Chiang, C.-Y. (2008). Human Tuberculosis Caused by Mycobacterium bovis, Taiwan. *Emerging Infectious Diseases*, 14(3), 515–517. <https://doi.org/10.3201/eid1403.070058>
- Lekko, Y., Che-Amat, A., Ooi, P., Omar, S., Ramanoon, S., Mazlan, M., Jesse, F., Jasni, S., & Ariff Abdul-Razak, M. (2021). Mycobacterium Tuberculosis and Avium Complex Investigation among Malaysian Free-Ranging Wild Boar and Wild Macaques at Wildlife-Livestock-Human Interface. *Animals*, 11(11), 3252. <https://doi.org/10.3390/ani11113252>
- Lipiec, M., Nowakowski, K., Radulski, Ł., Iwaniak, W., & Wazna, A. (2018). Badgers as a potential source of bovine tuberculosis – first studies in Poland. *Annals of Agricultural and Environmental Medicine*, 25(3), 409–410. <https://doi.org/10.26444/aaem/80984>
- Livingstone, P., Hancox, N., Nugent, G., Mackereth, G., & Hutchings, S. (2015). Development of the New Zealand strategy for local eradication of tuberculosis from wildlife and livestock. *New Zealand Veterinary Journal*, 63(sup1), 98–107. <https://doi.org/10.1080/00480169.2015.1013581>
- Macdonald, D. W., Riordan, P., & Mathews, F. (2006). Biological hurdles to the control of TB in cattle: A test of two hypotheses concerning wildlife to explain the failure of control. *Biological Conservation*, 131(2), 268–286. <https://doi.org/10.1016/j.biocon.2006.05.006>
- Machackova, M., Matlova, L., Lamka, J., Smolik, J., Mmelicharek, I., Hanzalikova, M., Docekal, J., Cvetnik, Z., Nagy, G., Lipiec, M., Ocepek, M., & Pavlik, I. (2003). Wild boar (Sus scrofa) as a possible vector of mycobacterial infections: review of literature and critical analysis of data from Central Europe between 1983 to 2001. *Veterinárni Medicína*, 48(3), 51–65. <https://doi.org/10.17221/5750-vetmed>
- Marais, B. J., Buddle, B. M., Klerk-Lorist, L., Nguipod-Djomo, P., Quinn, F., & Greenblatt, C. (2019). BCG vaccination for bovine tuberculosis; conclusions from the Jerusalem One Health workshop. *Transboundary and Emerging Diseases*, 66(2), 1037–1043. <https://doi.org/10.1111/tbed.13089>
- Marco, V., Marianelli, C., Russo, M., Aronica, V., Bollo, E., Amedeo, S., Valenza, F., & Capucchio, M. T. (2008). Black Wild Pigs of Nebrodi Park in Sicily: Evidence of Their Possible Role as Reservoir of Mycobacterium Tuberculosis Complex Infection. *ESVP; ESVP*, 84.
- Martín-Hernando, M. P., Höfle, U., Vicente, J., Ruiz-Fons, F., Vidal, D., Barral, M., Garrido, J. M., de la Fuente, J., & Gortazar, C. (2007). Lesions associated with Mycobacterium tuberculosis complex infection in the European wild boar. *Tuberculosis*, 87(4), 360–367. <https://doi.org/10.1016/j.tube.2007.02.003>
- Meunier, N. V., Sebulime, P., White, R. G., & Kock, R. (2017). Wildlife-livestock interactions and risk areas for cross-species spread of bovine tuberculosis. *Onderstepoort Journal of Veterinary Research*, 84(1), 1221. <https://doi.org/10.4102/ojvr.v84i1.1221>
- Morris, R. S., Pfeiffer, D. U., & Jackson, R. (1994). The epidemiology of Mycobacterium bovis infections. *Veterinary Microbiology*, 40(1–2), 153–177. [https://doi.org/10.1016/0378-1135\(94\)90053-1](https://doi.org/10.1016/0378-1135(94)90053-1)
- Müller, B., Dürr, S., Alonso, S., Hattendorf, J., Laisse, C. J. M., Parsons, S. D. C., van Helden, P. D., & Zinsstag, J. (2013). Zoonotic Mycobacterium bovis-induced Tuberculosis in Humans. *Emerging Infectious Diseases*, 19(6), 899–908. <https://doi.org/10.3201/eid1906.120543>
- Müller, M., Naumann, L., Weber, A., Ehrlein, J., Ewingmann, T., Krisch, A., & Kahlau, D. (2007). Detection of Mycobacterium tuberculosis Complex in Wild Boars by PCR. *Tierärztliche Umschau*, 62(3), 140–143.
- Naranjo, V., Gortazar, C., Vicente, J., & de la Fuente, J. (2008). Evidence of the role of European wild boar as a reservoir of Mycobacterium tuberculosis complex. *Veterinary Microbiology*, 127(1–2), 1–9. <https://doi.org/10.1016/j.vetmic.2007.10.002>
- Neill, S. D., Skuce, R. A., & Pollock, J. M. (2005). Tuberculosis - new light from an old window. *Journal of Applied Microbiology*, 98(6), 1261–1269. <https://doi.org/10.1111/j.1365-2672.2005.02599.x>
- Nishi, J. S., Shury, T., & Elkin, B. T. (2006). Wildlife reservoirs for bovine tuberculosis (Mycobacterium bovis) in Canada: Strategies for management and research. *Veterinary Microbiology*, 112(2–4), 325–338. <https://doi.org/10.1016/j.vetmic.2005.11.013>
- O'Brien, D. J., Schmitt, S. M., Fitzgerald, S. D., Berry, D. E., & Hickling, G. J. (2006). Managing the wildlife reservoir of Mycobacterium bovis: The Michigan, USA, experience. *Veterinary Microbiology*, 12(2–4), 313–323. <https://doi.org/10.1016/j.vetmic.2005.11.014>

- Olea-Popelka, F., Muwonge, A., Perera, A., Dean, A. S., Mumford, E., Erlacher-Vindel, E., Forcella, S., Silk, B. J., Ditiu, L., El Idrissi, A., Raviglione, M., Cosivi, O., LoBue, P., & Fujiwara, P. I. (2017). Zoonotic tuberculosis in human beings caused by *Mycobacterium bovis* —a call for action. *The Lancet Infectious Diseases*, 17(1), e21–e25.
[https://doi.org/10.1016/s1473-3099\(16\)30139-6](https://doi.org/10.1016/s1473-3099(16)30139-6)
- Oloya, J., Opuda-Asibo, J., Kazwala, R., Demelash, A. B., Skjervea, E., LUND, A., Johansen, T. B., & Djonneb, B. (2008). *Mycobacteria* causing human cervical lymphadenitis in pastoral communities in the Karamoja region of Uganda. *Epidemiology and Infection*, 136(5), 636–643.
<https://doi.org/10.1017/s0950268807009004>
- Organization, W. H. (2014). *Basic facts on tuberculosis (TB) in the WHO European Region*.
- Palmer, M. V., Waters, W. R., & Whipple, D. L. (2002). Lesion Development in White-tailed Deer (*Odocoileus virginianus*) Experimentally Infected with *Mycobacterium bovis*. *Veterinary Pathology*, 39(3), 334–340. <https://doi.org/10.1354/vp.39-3-334>
- Pate, M., Zajc, U., Pirš, T., Ocepek, M., & Krt, B. (2024). Bovine Tuberculosis in Wild Boar (*Sus scrofa*) in Slovenia. *Journal of Wildlife Diseases*, 60(2), 537–541. <https://doi.org/10.7589/jwd-d-23-00123>
- Pavlik, I. (2006). The experience of new European Union Member States concerning the control of bovine tuberculosis. *Veterinary Microbiology*, 112(2–4), 221–230.
<https://doi.org/10.1016/j.vetmic.2005.11.024>
- Pérez de Val, B., Napp, S., Velarde, R., Lavín, S., Cervera, Z., Singh, M., Allepuz, A., & Mentaberre, G. (2017). Serological Follow-up of Tuberculosis in a Wild Boar Population in Contact with Infected Cattle. *Transboundary and Emerging Diseases*, 64(1), 275–283. <https://doi.org/10.1111/tbed.12368>
- Phillips, C. J. C., Foster, C. R. W., Morris, P. A., & Teverson, R. (2003). The transmission of *Mycobacterium bovis* infection to cattle. *Research in Veterinary Science*, 74(1), 1–15.
[https://doi.org/10.1016/s0034-5288\(02\)00145-5](https://doi.org/10.1016/s0034-5288(02)00145-5)
- Pollock, J. M., Rodgers, J. D., Welsh, M. D., & McNair, J. (2006). Pathogenesis of bovine tuberculosis: The role of experimental models of infection. *Veterinary Microbiology*, 112(2–4), 141–150.
<https://doi.org/10.1016/j.vetmic.2005.11.032>
- Queirós, J., Alves, P. C., Vicente, J., Gortázar, C., & de la Fuente, J. (2018). Genome-wide associations identify novel candidate loci associated with genetic susceptibility to tuberculosis in wild boar. *Scientific Reports*, 8(1), 20158.
<https://doi.org/10.1038/s41598-018-20158-x>
- Réveillaud, É., Desvaux, S., Boschirol, M.-L., Hars, J., Faure, É., Fediaevsky, A., Cavalerie, L., Chevalier, F., Jabert, P., Poliak, S., Tourette, I., Hendrikx, P., & Richomme, C. (2018). Infection of Wildlife by *Mycobacterium bovis* in France Assessment Through a National Surveillance System, Sylvatub. *Frontiers in Veterinary Science*, 5, 262.
<https://doi.org/10.3389/fvets.2018.00262>
- Sandoval Barron, E., Swift, B., Chantrey, J., Christley, R., Gardner, R., Jewell, C., McGrath, I., Mitchell, A., O’Cathail, C., Prosser, A., Ridout, S., Sanchez-Cabezudo, G., Smith, N., Timofte, D., Williams, N., & Bennett, M. (2018). A study of tuberculosis in road traffic-killed badgers on the edge of the British bovine TB epidemic area. *Scientific Reports*, 8(1), 17206. <https://doi.org/10.1038/s41598-018-35652-5>
- Sannino, E., Cardillo, L., Paradiso, R., Cerrone, A., Coppa, P., Toscano, V. M., D’Alessio, N., Lucibelli, M. G., Galiero, G., de Martinis, C., & Fusco, G. (2021). A correlation of *Mycobacterium bovis* SB0134 infection between cattle and a wild boar (*Sus Scrofa*) in Campania region. *Veterinary and Animal Science*, 13, 100182.
<https://doi.org/10.1016/j.vas.2021.100182>
- Santos, N., Colino, E. F., Arnal, M. C., de Luco, D. F., Sevilla, I., Garrido, J. M., Fonseca, E., Valente, A. M., Balseiro, A., Queirós, J., Almeida, V., Vicente, J., Gortázar, C., & Alves, P. C. (2022). Complementary roles of wild boar and red deer to animal tuberculosis maintenance in multi-host communities. *Epidemics*, 41, 100633.
<https://doi.org/10.1016/j.epidem.2022.100633>
- Santos, N., Nunes, T., Fonseca, C., Vieira-Pinto, M., Almeida, V., Gortázar, C., & Correia-Neves, M. (2018). Spatial Analysis of Wildlife Tuberculosis Based on a Serologic Survey Using Dried Blood Spots, Portugal. *Emerging Infectious Diseases*, 24(12), 2169–2175.
<https://doi.org/10.3201/eid2412.171357>
- Scherer, C., Radchuk, V., Staubach, C., Müller, S., Blaum, N., Thulke, H., & Kramer-Schadt, S. (2019). Seasonal host life-history processes fuel disease dynamics at different spatial scales. *Journal of Animal Ecology*, 88(11), 1812–1824.
<https://doi.org/10.1111/1365-2656.13070>
- Schulz, G., Deuter, H., & Dedek, J. (1992). Occurrence of *Mycobacterium bovis* Infection in Free-Living Wild Boar. *Verh. Ber. Erkr. Zootiere*, 51–53.
- Shimao, T. (2010). Control of Cattle TB in Japan. *Kekkaku: [Tuberculosis]*, 85(8), 661–666.
- Sichewo, P. R., Michel, A. L., Musoke, J., & Etter, E. M. C. (2019). Risk Factors for Zoonotic Tuberculosis at the Wildlife–Livestock–Human Interface in South Africa. *Pathogens*, 8(3), 101.
<https://doi.org/10.3390/pathogens8030101>

- Srinivasan, S., Easterling, L., Rimal, B., Niu, X. M., Conlan, A. J. K., Dudas, P., & Kapur, V. (2018). Prevalence of Bovine Tuberculosis in India: A systematic review and meta-analysis. *Transboundary and Emerging Diseases*, 65(6), 1627–1640. <https://doi.org/10.1111/tbed.12915>
- Stefano, G., Cristina, B., Andrea, D., Massimo, D. C., & Maurizio, C. (2006). La tubercolosi nell'ecosistema della fauna selvatica e domestica nella regione Marche. *L'Osservatorio*.
- Thoen, C., LoBue, P., & de Kantor, I. (2006). The importance of Mycobacterium bovis as a zoonosis. *Veterinary Microbiology*, 112(2–4), 339–345. <https://doi.org/10.1016/j.vetmic.2005.11.047>
- Varela-Castro, L., Sevilla, I. A., Payne, A., Gilot-Fromont, E., & Barral, M. (2021). Interaction Patterns between Wildlife and Cattle Reveal Opportunities for Mycobacteria Transmission in Farms from North-Eastern Atlantic Iberian Peninsula. *Animals*, 11(8), 2364. <https://doi.org/10.3390/ani11082364>
- Vicente, J., Höfle, U., Garrido, J. M., Fernández-De-Mera, I. G., Juste, R., Barral, M., & Gortazar, C. (2006). Wild boar and red deer display high prevalences of tuberculosis-like lesions in Spain. *Veterinary Research*, 37(1), 107–119. <https://doi.org/10.1051/vetres:2005044>
- Vicente, J., Höfle, U., Garrido, J. M., Fernández-de-mera, I. G., Acevedo, P., Juste, R., Barral, M., & Gortazar, C. (2007). Risk factors associated with the prevalence of tuberculosis-like lesions in fenced wild boar and red deer in south central Spain. *Veterinary Research*, 38(3), 451–464. <https://doi.org/10.1051/vetres:2007002>
- Vicente, J., Höfle, U., Garrido, J. M., Fernández-De-Mera, I. G., Juste, R., Barral, M., & Gortazar, C. (2006). Wild boar and red deer display high prevalences of tuberculosis-like lesions in Spain. *Veterinary Research*, 37(1), 107–119. <https://doi.org/10.1051/vetres:2005044>
- Walker, H. L., Miller, R. S., Pomeroy, L. W., & Arruda, A. G. (2025). Characterizing risk factors for infection of Mycobacterium bovis between wild pigs and domestic cattle from an outbreak response California, 1961–1967. *Preventive Veterinary Medicine*, 235, 106399. <https://doi.org/10.1016/j.prevetmed.2024.106399>
- Welz, M., Anusz, K., Salwa, A., Zaleska, M., Bielecki, W., Osińska, B., Kaczor, S., & Kita, J. (2005). Bovine Tuberculosis in European Bison in the Bieszczady Region. *Med Wet*, 61(4), 441–444.
- World Health Organization. (2020). *Global Tuberculosis Report 2020*.
- Zanella, G., Durand, B., Hars, J., Moutou, F., Garin-Bastuji, B., Duvauchelle, A., Fermé, M., Karoui, C., & Boschioli, M. L. (2008). MYCOBACTERIUM BOVIS IN WILDLIFE IN FRANCE. *Journal of Wildlife Diseases*, 44(1), 99–108. <https://doi.org/10.7589/0090-3558-44.1.99>
- Zanetti, S., Bua, A., Molicotti, P., Delogu, G., Mura, A., Ortu, S., & Sechi, L. (2008). Identification of mycobacterial infections in wild boars in Northern Sardinia, Italy. *Acta Veterinaria Hungarica*, 56(2), 145–152. <https://doi.org/10.1556/avet.56.2008.2.1>
- Zimpel, C. K., Patané, J. S. L., Guedes, A. C. P., de Souza, R. F., Silva-Pereira, T. T., Camargo, N. C. S., de Souza Filho, A. F., Ikuta, C. Y., Neto, J. S. F., Setubal, J. C., Heinemann, M. B., & Guimaraes, A. M. S. (2020). Global Distribution and Evolution of Mycobacterium bovis Lineages. *Frontiers in Microbiology*, 11, 843. <https://doi.org/10.3389/fmicb.2020.00843>