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A review of bovine tuberculosis transmission risk in European wildlife communities

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REVIEW

A review of bovine tuberculosis transmission risk in European wildlife communities

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ABSTRACT

1. Understanding how disease moves through wildlife communities is essential to managing outbreaks of zoonotic diseases across the globe. Bovine tuberculosis is a disease caused by the bacterium *Mycobacterium bovis* that can threaten domestic and wildlife species. The mechanism by which *Mycobacterium bovis* is spread between species is still poorly understood. Previous reviews are limited in the breadth of species considered and are primarily concerned with transmission from wildlife to domestic species.
2. We conducted a review and analysis of *Mycobacterium bovis* prevalence rates in European wildlife species to identify species of concern for the transmission of bovine tuberculosis in a wildlife community. We subsequently conducted a narrative review of these species assessing the risk of *Mycobacterium bovis* transmission in a wildlife community based on available literature.
3. We calculated weighted mean disease prevalence rates to be highest in fallow deer (*Dama dama*, 20%), Eurasian badgers (*Meles meles*, 11%), wild boar (*Sus scrofa*, 9%) and red foxes (*Vulpes vulpes*, 4%). We considered these species to be of particular concern for the transmission of *Mycobacterium bovis* and selected them as the focus of our narrative review and risk assessment. Our risk assessment considered disease pathology, spatiotemporal activity patterns and animal behaviour as factors affecting the likelihood of *Mycobacterium bovis* transmission between wildlife species.
4. We found that prior research has principally focused on a few individual species, but that *Mycobacterium bovis* transmission through a wildlife community is likely more complex. We determined that disease transmission between multiple species may compound the severity of an outbreak of bovine tuberculosis. Broad, multi-species sampling campaigns and standardised *Mycobacterium bovis* testing protocols should be implemented in future studies. We also determined that an in-depth analysis of spatiotemporal overlap between species was needed to better assess the risk of transmission between wildlife species.

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INTRODUCTION

The importance of understanding disease ecology has become starkly evident in recent years as the COVID-19 pandemic dramatically demonstrated the severe impact that disease can cause across all aspects of human life (Decerf et al. 2020). It was also a reminder that humanity remains inextricably linked with wildlife. The pandemic began with zoonotic transmission from wildlife, subsequently spread among and between human populations and has now infected other wildlife species (Shereen et al. 2020, Chandler et al. 2021). Although the COVID-19 pandemic is now one of the most infamous examples of a zoonotic disease, smallpox, AIDS, Ebola virus, SARS, MERS and plague are all diseases which originated in animal species and are a threat to human health (Keesing & Ostfeld 2021). The economic impact of a disease outbreak can also be severe, with impacts from the level of an individual farm to national economies and international trade (Thoen et al. 2006). In England, an outbreak of bovine tuberculosis costs farmers an average of £57776 (Butler et al. 2010). National eradication programs in Ireland cost £1 billion from 1954 to 1988 and was still considered to have saved the country a considerable sum compared to the economic losses the uncontrolled spread of bovine tuberculosis might have caused (Thoen et al. 2006). The spread of disease may also threaten at-risk species and reduce global biodiversity (Thorne & Williams 1988, Skerratt et al. 2007, Grogan & Kelly 2013). Furthermore, it is likely that decreasing biodiversity will cause outbreaks of disease to become even more frequent and destructive (Pongsiri et al. 2009). Understanding how disease spreads among wildlife communities is essential to managing the threat they pose to humans and wildlife.

The bacterium *Mycobacterium bovis* is the causative agent in bovine tuberculosis, a disease that poses a risk to the health of livestock, humans and wildlife globally (Hardie & Watson 1992). Bovine tuberculosis is characterised by the progressive development of lesions in the lungs, lymph nodes or other organs and may spread through various bodily excretions (Ayele et al. 2004). Bovine tuberculosis in wildlife often begins with non-visible lesions (NVLs) localised to the origin of infection and may remain in this state for an extended period (Delahay et al. 2001, Corner 2006, Gavier-Widén et al. 2009). If the pathology becomes more severe, the host may develop generalised gross lesions, shed bacilli through multiple routes, exhibit altered behaviour and ultimately die (Corner 2006, Millán et al. 2008). The exact progression of the disease may vary and is likely driven by factors such as species, age and route of infection (Gavier-Widén et al. 2009). The presence of *Mycobacterium bovis* in wildlife species usually originates from infected livestock herds but may thereafter spread between wildlife species and back to livestock (Romero et al. 2008, Réveillaud et al. 2018, O'Hare et al. 2021, Swift et al. 2021). Infected wildlife populations may be considered either maintenance or spillover hosts (Corner 2006). Maintenance hosts can sustain a baseline of infection in the population without additional inputs from another species, whereas spillover hosts cannot maintain infection in the population without re-infection from another species (Corner 2006). Maintenance hosts are generally considered to be of greater concern (Delahay et al. 2001), but both types of infected populations can further the spread of disease.

The mechanism by which *Mycobacterium bovis* is spread between species is still poorly understood, though there is potential for both direct and indirect transmission. Infected animals may excrete *Mycobacterium bovis* in their saliva, urine or faeces and bacilli may persist in the environment for up to 80 days (Sweeney et al. 2007, Corner et al. 2011, Fine et al. 2011, King et al. 2015). Animals may become infected through bites, aerosol transmission or ingestion of infected materials (Corner 2006, Corner et al. 2011, Richomme et al. 2020). Many wildlife species have been shown to persist with a latent form of infection characterised by no visible macroscopic lesions (NVLs), symptoms localised to the origin of infection and little shedding of colony-forming units (CFUs) (O'Brien et al. 2006, Delahay et al. 2007, Gavier-Widén et al. 2009, Payne et al. 2012). It is only when the disease has become more advanced and systemic that high numbers of CFUs may be shed through multiple routes (Corner 2006, Michelet et al. 2018).

In this study, we identified likely hosts and mechanisms involved in the transmission of *Mycobacterium bovis* in a European wildlife community. The prevalence of *Mycobacterium bovis* infection in a population is often used as a general indicator of transmission risk in wildlife but this disease prevalence data has not been analysed across studies (Delahay et al. 2001, 2007). We conducted a review and analysis of bovine tuberculosis disease prevalence rates in European wildlife to identify species of concern and subsequently synthesised and discussed how those species might contribute to transmission of bovine tuberculosis in a wildlife community. We evaluated the risk of bovine tuberculosis transmission between species based on their pathologies, spatiotemporal activity patterns and behaviours.

METHODS FOR IDENTIFYING SPECIES OF CONCERN

We conducted a review of *Mycobacterium bovis* prevalence rates in European wildlife to identify species of concern for transmission of *Mycobacterium bovis* in a wildlife

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community. Disease prevalence is the proportion of infected to uninfected individuals in a population. We considered species with a high prevalence of bovine tuberculosis in their populations to be of particular concern for transmission of the disease. We only included those populations which had at least one positive case of bovine tuberculosis because only infected populations are relevant to understanding disease transmission in wildlife.

Literature searches

We conducted a series of systematic searches to collect bovine tuberculosis disease prevalence rates of European wildlife species, using broad search terms in the CAB, ProQuest, JSTOR, Science Direct and Web of Science databases (Appendix S1). The data collected were the raw numbers of animals tested for *Mycobacterium bovis* infection and those that tested positive, from which we calculated disease prevalence rates. We did not include data from tests for other species of Mycobacterium. We limited our search to peer-reviewed articles in academic journals which were available in English.

Eligibility criteria

Papers which used simulated data, case studies, captive population or pooled data from multiple regions were excluded. Furthermore, we did not include papers that duplicated a dataset which was already included in the analysis. We initially selected papers by title and abstract, then further refined them by reading the full text (Fig. 1). We selected papers which reported the number of animals tested for *Mycobacterium bovis* and those positive for *Mycobacterium bovis* infection. We also selected those papers from which we could calculate the required data given the information provided (i.e. calculating the number of *Mycobacterium bovis* positive animals from a given prevalence rate and the number of tested animals). From an initial 1830 publications, we selected 92 papers for inclusion in the final analysis (Appendix S2).

Estimating disease prevalence

We calculated the mean prevalence for species that had been surveyed a minimum of 10 times to attain reliable results (Appendix S3). Since we were primarily interested in the severity of infection in a population, we restricted our calculations to surveys that contained at least one animal that tested positive for *Mycobacterium bovis*. Due to the large variability in sample size between surveys (549 ± 1562 individuals/survey ± SD, min–max = 1–11599 individuals/survey), we weighed mean prevalence by sample size so that surveys with larger sample sizes had a greater

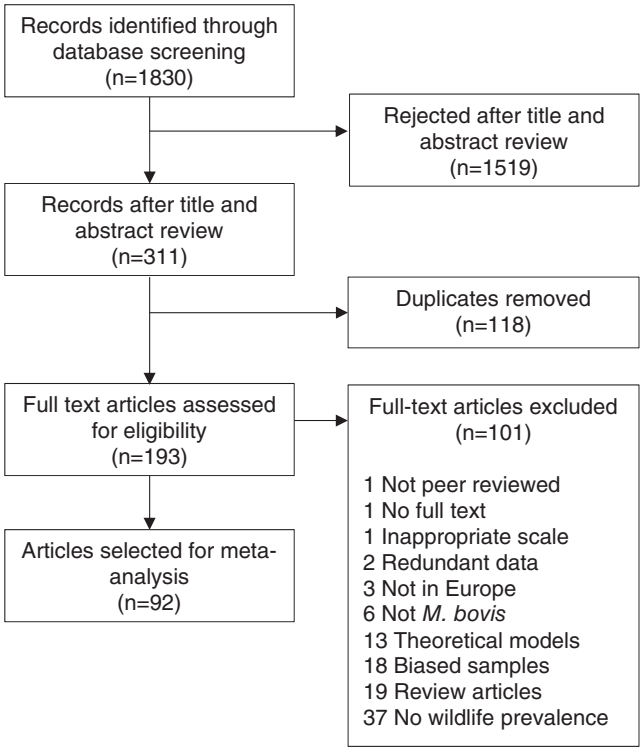

Fig. 1. Paper selection process for the review of *Mycobacterium bovis* prevalence data.

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impact on the final prevalence estimates (Galmiche et al. 2019, O'Brien et al. 2019). We calculated weighted means using the following formula:

$$P_w = \frac{\Sigma(P_i \cdot N_i)}{N_t}$$

where P_w is weighted mean prevalence, P_i is the percent prevalence of an individual survey, N_i is the sample size of an individual survey, and N_t is the total number of animals sampled for a species. Following the analysis results, we selected those species with the highest disease prevalence for further analysis of transmission risk.

DISEASE PREVALENCE – RESULTS

Many of the selected papers contained multiple surveys of disease prevalence in wildlife (mean ± SD = 7.2 ± 10.2 surveys/study, min–max = 1–56 surveys/study), which provided a large database from which to conduct the analysis. We collected data from 661 surveys of bovine tuberculosis prevalence rates in wildlife, which covered about 50 species (some surveys did not identify beyond the genus). Data from 12 nations were included in the final analysis, of which 85% of surveys were conducted in either the United Kingdom and Ireland or the Iberian Peninsula (Fig. 2). The publication dates of selected papers ranged across a period of 36 years (1985–2021) (Appendix S4).

Fallow deer (*Dama dama*) had the highest weighted mean disease (±SD) prevalence (20.10 ± 0.55%, $n = 14$ studies), followed by Eurasian badgers (*Meles meles*, 11.04 ± 0.12%, $n = 36$), wild boar (*Sus scrofa*, 8.96 ± 0.22%, $n = 35$) and red foxes (*Vulpes vulpes*, 3.55 ± 0.20%, $n = 12$, Fig. 3). The Iberian lynx had a high weighted mean disease prevalence but was excluded from the ranking due to a low total sample size (i.e. one individual per survey). Fallow deer also had the highest proportion (88%) of populations that were infected with *Mycobacterium bovis*, followed by wild boar (87%), badgers (80%), foxes (61%), red deer (58%) and roe deer (53%).

The majority of individuals sampled were red deer (100685), followed by wild boar (64037) and badgers (60594), but badger populations were surveyed more frequently than other species (232 surveys, Fig. 4). Badgers were surveyed most often in the UK and Ireland, which accounted for 86% of all badger surveys (Fig. 5). The Iberian Peninsula was the most common region for surveys of wild boar, red deer, red fox and fallow deer (Fig. 5). Roe deer were surveyed most frequently in France (Fig. 5).

DISEASE PREVALENCE – DISCUSSION

The high prevalence of *Mycobacterium bovis* in infected fallow deer populations is perhaps the most surprising result, as their importance as a host species has not been emphasised compared to badgers, wild boar or red deer. This result certainly calls for further research into the role that fallow deer play in the disease ecology of bovine tuberculosis. Furthermore, the low disease prevalence found in red deer along with the relatively low percentage of infected populations may suggest that their contribution to the spread and maintenance of *Mycobacterium bovis* is smaller than their large share of research effort might suggest. However, other factors like population size and the details of disease progression within a host contribute to the importance of a species in the ecology of a disease, and one should be careful extrapolating too far based on prevalence data alone (Delahay et al. 2001, Corner 2006).

The contributions of the wildlife community to the disease ecology of bovine tuberculosis are likely underestimated due to a paucity of data. Though the scope of the pooled data included about 50 species, only six had sufficient data to allow for analysis. Thirteen species were only surveyed once, while badgers were surveyed 232 times. This unequal distribution of research effort may have reasonable founding, but it serves well to illustrate how myopic research trends may become. These trends may also be regionally specific. Of the surveys conducted in the UK and Ireland, 67% were of badgers. Comparatively, wild boar were the most surveyed species in the Iberian Peninsula, accounting for 39% of the surveys in that region. While mammalian diversity is low in the UK compared to other parts of Europe, the emphasis of British studies on badgers is leaving many other species under surveyed, though broader sampling efforts may return surprising results (Delahay et al. 2007). Multi-species sampling should become a more frequent practice, especially in the UK and Ireland, if we are to better understand the disease ecology of bovine tuberculosis.

Though our analysis benefits from a breadth in scope, it is also limited by it. There was a large degree of variation in survey sample size and the number of surveys per species. Our analysis could not account for variation in the number of populations per survey or variation in ecosystems surveyed. Some variation in prevalence estimates could be reduced in future reviews if standardised sampling and testing protocols were produced. Future reviews could also provide more robust estimates of disease prevalence for understudied species as new studies contribute additional data.

We selected Eurasian badgers, wild boar, fallow deer and red foxes for a more detailed analysis of transmission risk. Our analysis revealed that these species have high disease

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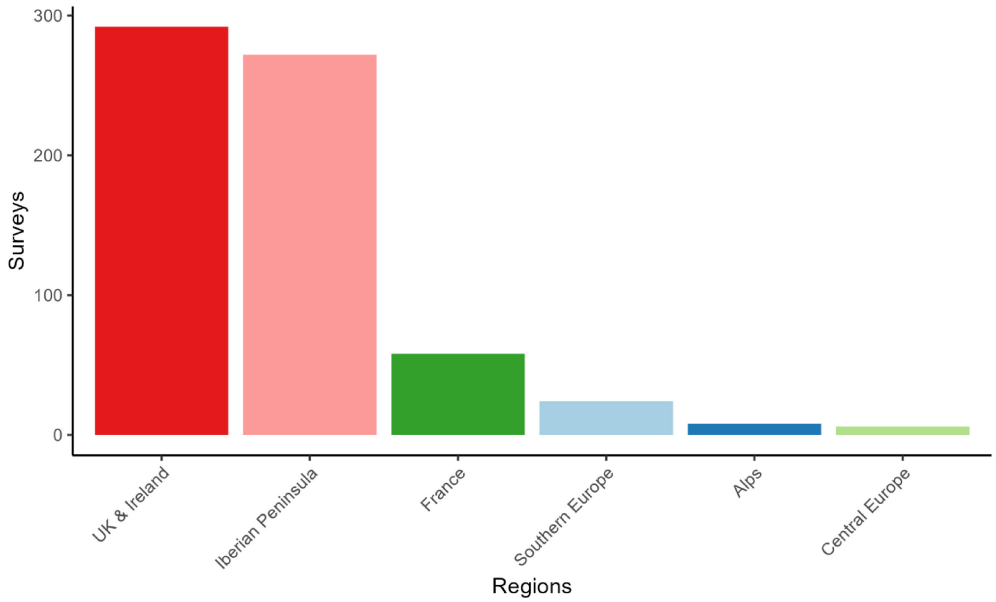

Fig. 2. Study site locations of the studies included in the analysis. Region definitions are as follows: Alps = Switzerland, Austria and Liechtenstein; UK & Ireland = United Kingdom and Ireland; Central Europe = Germany, Poland and the Netherlands; Iberian Peninsula = Portugal and Spain; Southern Europe = Italy and Slovenia.

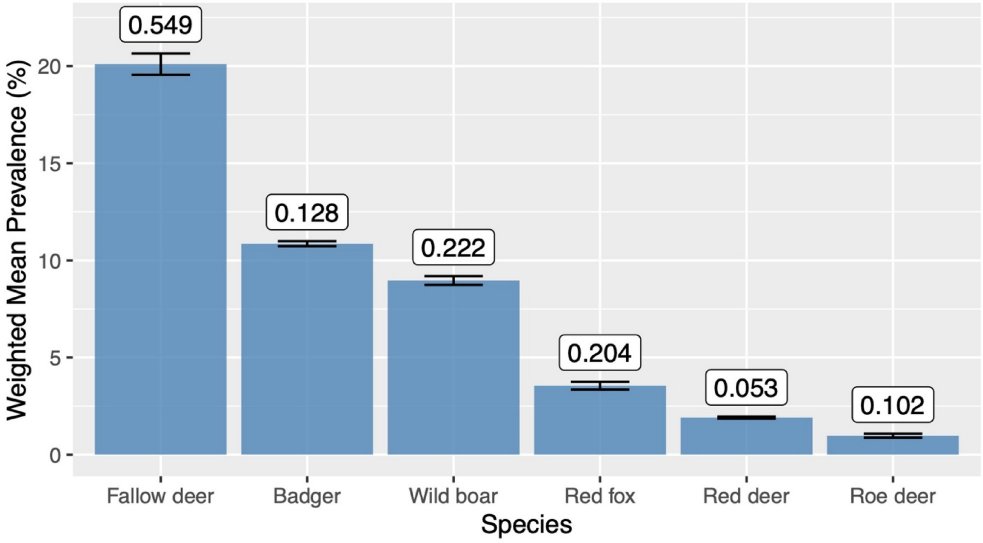

Fig. 3. Weighted mean prevalence of bovine tuberculosis in infected wildlife populations. Error bars show standard deviation with the value above.

prevalence rates and, therefore, warrant further investigation into their suitability as wildlife hosts of *Mycobacterium bovis*.

EVALUATION OF TRANSMISSION RISK

When evaluating species for transmission risk, it is common to assess each species independently of the wildlife community in which it occurs (Corner 2006). While this method may be necessary when evaluating species from across the globe, we contend that animals should be considered in context whenever possible. Since the species of concern we identified in our analysis are often found in the same wildlife communities, we evaluated both their individual contributions to disease transmission risk and what effects might arise from their interactions with one another.

Pathology and epidemiology

Understanding the typical course of bovine tuberculosis in a species is of central importance for assessing the

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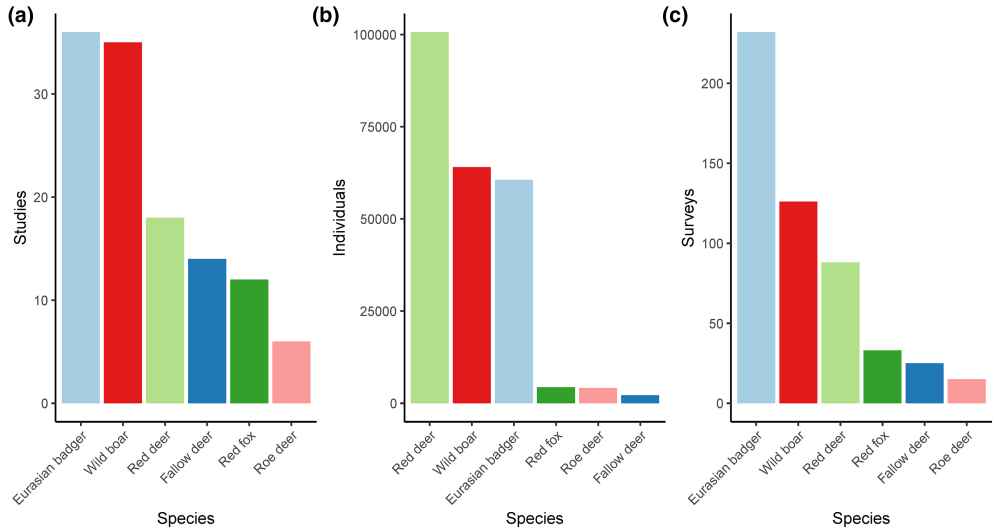

Fig. 4. Numbers of (a) studies, (b) individual animals sampled and (c) surveys for the major species.

risk of transmission (Delahay et al. 2001, Corner 2006). The length of time during which an individual sheds bacilli, the number of bacilli shed, and the routes of excretion all contribute to the risk that an infected individual poses to the wildlife community (Delahay et al. 2001). The susceptibility of an individual to infection and subsequent transmission may be evaluated by understanding common routes of infection, lesion structure and location, and the routes and level of excretion (Corner 2006). At the population level, disease prevalence and severity are factors which may affect transmission (Corner 2006).

We found disease prevalence rates to be high (weighted mean of 11%) among infected populations of Eurasian badgers, and most of these animals will present NVLs (non-visible lesions) (Kelly et al. 2010, Murphy et al. 2010). Most badgers are infected by aerosol through the respiratory tract, though some may become infected from bites (Gallagher & Clifton-Hadley 2000, Murphy et al. 2010, Courcier et al. 2018). Badgers with latent infection can persist for years with limited sites of infection and low numbers of bacilli in infected tissues (Corner et al. 2011). The localised nature of the infection, low bacilli count in infected tissues and relatively small body mass of badgers suggests that badgers at this stage of infection will shed few CFUs (colony-forming units). When the infection advances to a later stage, badgers may exhibit macroscopic lesions, altered behaviour and shedding of bacilli through saliva, faeces and urine (Gallagher & Clifton-Hadley 2000, Corner 2006, Courcier et al. 2018). At this advanced stage, badgers are most likely to infect other species. Badger-to-badger infection may occur from constant exposure to individuals with latent infection, as prevalence rates get progressively higher with age (Woodroffe et al. 2005).

The relationship between fallow deer and *Mycobacterium bovis* has been studied less than in badgers, but research suggests that their populations exhibit relatively high disease prevalence rates (weighted mean of 20%) when infected (Aranaz et al. 2004, García-Jiménez et al. 2013, Amato et al. 2016). Recent evidence from Ireland suggests that deer species may serve as maintenance hosts of bovine tuberculosis at high densities (Kelly et al. 2021). Lesions in deer species are usually associated with the respiratory tract and the lymph nodes of the head and may present as NVL or macroscopic lesions (Corner 2006, Gavier-Widén et al. 2009). The common presence of respiratory lesions suggests aerosol as the usual route of infection. Infected fallow deer tend to develop thinly encapsulated granulomas filled with high counts of bacilli, which puts them at a high risk of excretion (Johnson et al. 2008). Granulomas in the lungs of fallow deer may be more widespread compared to more localised lesions in other deer species (Aranaz et al. 2004). Deer species have also been observed shedding *Mycobacterium bovis* through multiple routes, including saliva and faeces (Lugton et al. 1998). The higher body mass of fallow deer relative to smaller mammals like badgers may also contribute to a higher number of CFUs being excreted into the environment (Ward et al. 2009).

Wild boar have weighted mean disease prevalence rates of 9% in infected populations. Though they can present with NVLs, visible lesions are common in infected animals, usually beginning in the mandibular lymph nodes and spreading into retropharyngeal and mesenteric lymph nodes as the disease progresses (Santos et al. 2009, García-Jiménez et al. 2015, Matos et al. 2016, Réveillaud et al. 2018). The prevalence of lesions in the mandibular lymph nodes suggests that an oral origin of infection is common, though the results of Parra et al. (2006)

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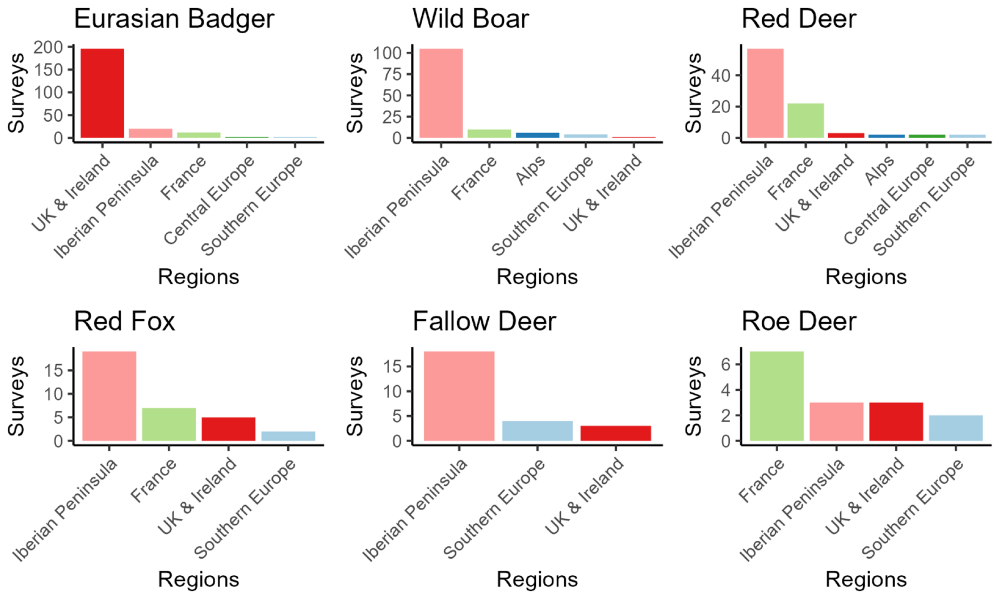

Fig. 5. Species survey locations for badger, wild boar, red deer, red fox, fallow deer and roe deer. Region definitions are as follows: Alps = Switzerland, Austria, and Liechtenstein; UK & Ireland = United Kingdom and Ireland; Central Europe = Italy and Slovenia.

demonstrate that a respiratory origin is also possible. Lesions are typically multifocal and may range from small capsulated lesions to large granulomas with a calcified necrotic centre (Parra et al. 2006, Santos et al. 2009, Matos et al. 2016). The capsulation of their lesions and a widespread immune response may reduce the number of bacilli shed by wild boar, but their large body mass and the frequency of large lesions suggest that they could shed substantial numbers of CFUs if the lesions open or the immune system fails (Parra et al. 2006). Open lesions draining into the salivary gland have been recorded in wild boar (Santos et al. 2009). In the advanced stages of infection when large lesions are widespread, wild boar have the potential to shed bacilli through multiple routes.

Though red foxes have lower disease prevalence rates (weighted mean of 4%) than Eurasian badgers, fallow deer and wild boar, they do have high disease prevalence rates compared to many other mammal species (Martin-Atance et al. 2005, Millán et al. 2008, Matos et al. 2016). Infected foxes usually present NVLs which are typical of a latent stage of disease, a state in which they may persist for some time (Michelet et al. 2018). Foxes usually have an oral origin of infection, which suggests the ingestion of infected materials (Millán et al. 2008, Richomme et al. 2020). The mesenteric lymph nodes are the typical site of infection in foxes (Michelet et al. 2018, Richomme et al. 2020). Foxes have been known to shed bacilli in saliva, faeces and urine, even without exhibiting macroscopic lesions (Michelet et al. 2018). Foxes that shed bacilli through multiple routes while presenting NVLs may well be considered "super-shedders" since they are likely to shed many bacilli over a lengthy period (Michelet et al. 2018). However, the relatively small body mass of foxes may put a limit on the number of CFUs that can be excreted at any given time.

Space use and activity patterns

To transmit *Mycobacterium bovis*, an individual must encounter infected materials. A degree of shared space use is, therefore, necessary for disease transmission. If an infected animal overlaps spatially and temporally with another, then there is an opportunity for direct transmission and indirect transmission. If two animals are using the same space, but at different times, then there is only the chance for indirect transmission. We examined studies of habitat preference and population density as metrics of space use while reviewing daily and seasonal activity patterns to determine the temporal use of those spaces.

Determining typical species activity patterns is valuable for understanding the potential for temporal overlap. Badgers and foxes share similar activity patterns and co-occur spatially (Fig. 6) (Torretta et al. 2016, Rossa et al. 2021). Badgers are nocturnal while fox activity typically ranges from nocturnal to crepuscular (Caravaggi et al. 2018, Ogurtsov et al. 2018, Kammerle et al. 2020). The large degree of temporal overlap between foxes and badgers suggests that there is a potential for direct transmission of bovine tuberculosis between species. Though foxes and badgers are known to also overlap spatially, there are differences in their selection of specific habitats

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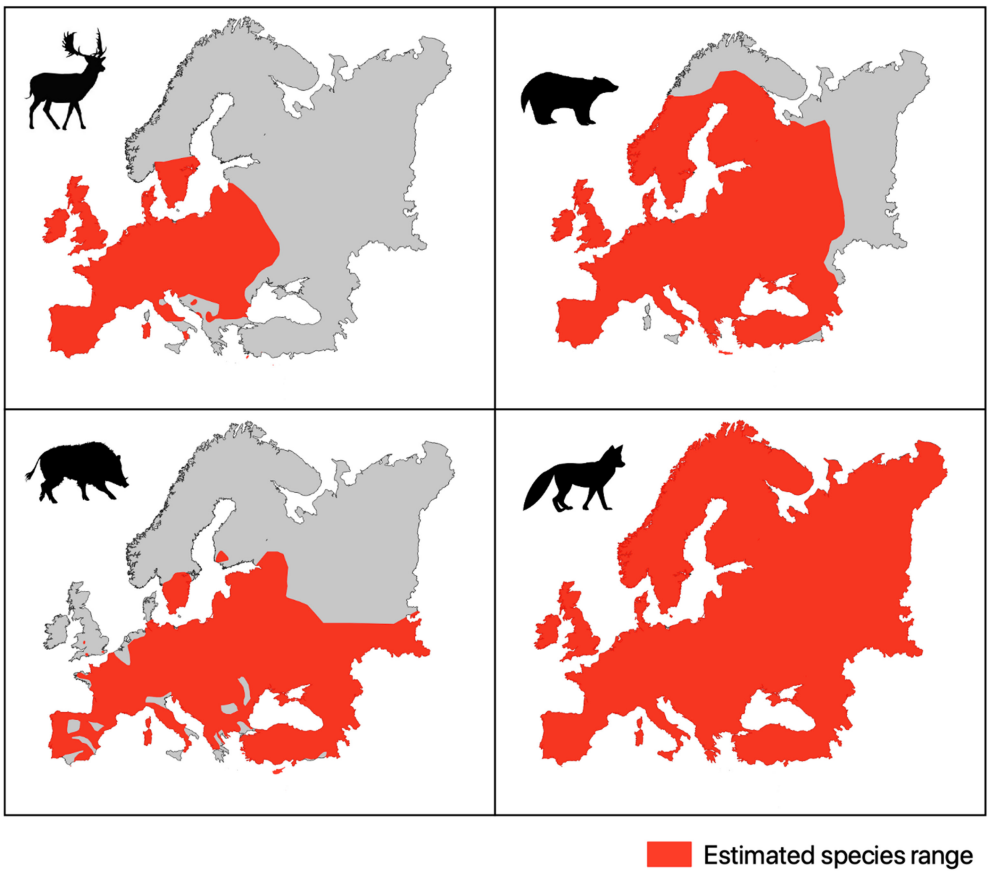

Fig. 6. The ranges of fallow deer, Eurasian badgers, wild boar and red foxes in Europe based on IUCN range data.

(Caravaggi et al. 2018). When denning, badgers prefer rich clay soils in mixed woodland, probably for ease of sett construction and density of invertebrate prey, while foxes prefer denning in coniferous woodland and have no soil preferences (Kurek et al. 2014). These species also exhibit differences in their typical social structures and home ranges, which are further shaped by the landscapes they inhabit (Parrott et al. 2012). Populations of foxes and badgers in upland habitats have larger ranges than populations in resource-rich, lowland habitats (Parrott et al. 2012). Badgers live in large family units with as many as 26 individuals per group (Woodroffe et al. 2009). Red foxes are mostly solitary but do maintain long-term social relationships among a community that shares a territorial space (Dorning & Harris 2019). Lowland habitats that support higher density populations of badgers and foxes may, therefore, be more vulnerable to outbreaks of bovine tuberculosis since they create increased spatial overlap both between and within host species.

Thickets, meadows and young forests are the most important habitat types for fallow deer, with meadow use increasing at night and during the winter (Borkowski & Pudełko 2007). Fallow deer are typically diurnal, but there is evidence to suggest that fallow deer attempt to avoid predation by adjusting their temporal activity patterns (Ciuti & Apollonio 2008, Caravaggi et al. 2018, Rossa et al. 2021). When fallow deer exhibit diurnal activity patterns, they may have limited temporal overlap with nocturnal/crepuscular species such as foxes, badgers and wild boar. However, the changes in fallow deer activity driven by the presence of predators, human disturbance or seasonal shifts may increase the degree of overlap between fallow deer and these other species. This may especially be true if multiple species are driven by these factors to align their activity patterns (Rossa et al. 2021). Fallow deer populations are present in most European countries, though their distribution is often spotty and centred around areas where the animals were originally introduced (Fig. 6). However, they are likely to overlap spatially with badgers, wild boar and foxes in many of the locations in which they occur, particularly given that their home ranges can extend to 9.75 km^2 (Chapman & Chapman 1980, Borkowski & Pudełko 2007, Caravaggi et al. 2018, Esattore et al. 2022). Their populations are expanding rapidly in Britain with the potential for a range increase from 25000 to 60000 km^2, possibly aided by

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increased habitat provided by broadleaf tree plantings (Ward 2005, Croft et al. 2019). Fallow deer may be solitary or associate in groups as large as 160 individuals, with group size highest in winter and spring (Thirgood 1996). Since high densities of deer are related to high densities of bovine tuberculosis and an increased likelihood of creating a maintenance population, the gregarious nature of fallow deer is of particular concern (Kelly et al. 2021).

Wild boar are nocturnal/crepuscular with a preference for woodland habitats (Merli & Meriggi 2006, Carrasco-Garcia et al. 2016, Ogurtsov et al. 2018). Wild boar may adjust their temporal activity patterns to avoid predation, as they have been shown to become increasingly nocturnal under hunting pressure or increasingly diurnal to avoid predation from wolves (Ohashi et al. 2013, Johann et al. 2020, Rossa et al. 2021). Wild boar will typically overlap temporally with badgers and foxes which are also nocturnal/crepuscular and spatially overlap with fallow deer, badgers and foxes (Caravaggi et al. 2018, Ogurtsov et al. 2018). Their groups vary in size and composition with the seasons, ranging from large family units in excess of 10 individuals in the summer to solitary or small mixed groups in the winter (Fernández-Llario et al. 1996, Maselli et al. 2014). Wild boar populations have been growing and expanding across Europe for several decades but are only present at a few locations in Britain such as Gloucestershire, Dorset and Kent/Sussex (Fig. 6) (Goulding et al. 2003, Wilson 2003, Dutton et al. 2015, Massei et al. 2015, Pittiglio et al. 2018). While wild boar have been reclaiming much of their historic range, there are challenges associated with their expansion which are exacerbated by the difficulty of monitoring their populations (Tack 2018, Markov et al. 2022). The unmarked expansion of wild boar into a region or the rapid increase in local wild boar populations may lead to an increased risk of disease transmission which may not be discovered for some time. The vulnerability of a wildlife community to disease outbreaks may change rapidly with changes to wildlife populations or human-driven alterations to the landscape, posing a serious challenge for research and management efforts which tend to move more slowly.

Denning, foraging and movement

A considerable amount of research has been done examining the behaviour of both wildlife and cattle in pastures and near farm buildings as a means of assessing the risk of *Mycobacterium bovis* transmission (Smith et al. 2008, Payne et al. 2016, 2017, Varela-Castro et al. 2021). Since much of the research into wildlife and *Mycobacterium bovis* has focused on badgers (35% of all surveys), our understanding of how disease transmission occurs in a wildlife community is rather limited (Macdonald et al. 2004, Sidorovich et al. 2011). Denning, foraging and movement are behaviours which represent the key daily activities of a wildlife community and pose different threats of disease transmission.

Dens and setts are enclosed, moist spaces which offer an ideal environment for the spread and survival of aerosolized bacilli (Sweeney et al. 2007). Since other species, such as red foxes, are known to den in badger setts, the sett itself may be a significant route by which infection is spread between wildlife species (Sidorchuk et al. 2015, Coppola et al. 2020, Nowakowski et al. 2020). Badgers and other species may also utilise the burrows of other animals, such as porcupines, and different species may inhabit a sett or burrow simultaneously (Coppola et al. 2020, Nowakowski et al. 2020). If predation occurs within the burrow and the soil is directly exposed to blood or other excreta, the risk of disease transmission could be considerable. Foxes are typically infected orally, so it seems unlikely that badgers are the common source of their infection (Millán et al. 2008, Richomme et al. 2020). However, foxes may be a source of infection for badgers. Foxes and badgers have also been observed spending time together near setts, even when foxes were not denning at that site, and appeared to leave the sett together (Macdonald et al. 2004). It is unknown what purpose this behaviour might serve, but it is possible that badgers and foxes associate with one another for foraging, similar to the American badger (*Taxidea taxus*) and coyote (*Canis latrans*) in North America (Minta et al. 1992, Thornton et al. 2018). Under certain conditions, badger populations will use latrines where they routinely urinate and defecate. Badger latrines may be a source of indirect infection since they are visited by multiple species, but latrine use may also limit the amount of infectious material accidentally ingested by animals when foraging (Smith et al. 2008, Varela-Castro et al. 2021).

Foraging presents an opportunity for direct and indirect disease transmission since animals may forage in the same habitat. Ingestion of infected materials or aerosolized bacilli while foraging is likely a major origin of infection for all species. Both badgers and foxes are generalist predators that eat what is locally abundant (Cresswell & Harris 1988, Díaz-Ruiz et al. 2013). In Britain, rabbits are the most important prey of foxes and earthworms are the primary prey of badgers (Kruuk & Parish 1981, Hofer 1986, Baker & Harris 2006, Webbon et al. 2006). Earthworms occur in high densities and are easiest for badgers to hunt in the short grass typical of grazed pastures (Kruuk & Parish 1981). Rabbits may be found in high densities in bracken and in woodland that borders open habitats (Hofer 1986). Woodland borders may, therefore, be an important intersection point between fox and badger foraging. Wild boar have a generalist diet that is primarily

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comprised of plant matter, with animal matter occupying a low percentage of the overall diet but one which is frequently present (Ballari & Barrios-García 2014). Forest fruits such as acorns and beech nuts are the most important elements of the wild boar diet during autumn and winter (Herrero et al. 2005). Where crops are available, they are heavily utilised by wild boar, especially in summer and autumn as crops reach maturity (Ballari & Barrios-García 2014). Wild boar may encounter badgers and foxes in agricultural land, forest edges or at carcass sites. Indeed, badgers, foxes and wild boar are all known scavengers, which may be a route of infection (Kruuk & Parish 1981, Herrero et al. 2005, Webbon et al. 2006, Sidorovich et al. 2011).

Fallow deer rely on grazing for graminoids for the bulk of their diet, though they also supplement with woodland browsing (Chapman & Chapman 1975, Obidziński et al. 2013). Grazing in livestock pasture may expose fallow deer to spatial overlap with badgers, whereas they may be more likely to encounter wild boar or foxes while browsing in woodlands. Fallow deer may ingest infected materials while grazing, but the pathogenesis of infection in deer suggests that aerosol is of greater concern than ingestion (Corner 2006). Their infected carcasses may also be a source of infection for scavenger species including wild boar, foxes and badgers. All species of concern forage in meadows and woodlands, so landscapes with an abundance of these habitat types may serve as ideal environments for transmission of bovine tuberculosis in the wildlife community. Yet not all foraging sites are determined by landscape. Supplementary feeding has been linked to the spread of bovine tuberculosis in other deer species and feed sites may act as hotspots of disease transmission where they occur (Miller et al. 2003). Livestock feed may serve a similar role in attracting wildlife and facilitating disease transmission between wildlife species. It's also possible that roads contribute to disease spread by routinely supplying carcasses to scavengers through traffic-related mortalities. Given these parameters, a human transformed patchwork landscape of livestock pasture, woodlands, agricultural lands and roads would offer the ideal landscape for the transmission of bovine tuberculosis to fallow deer, wild boar, badgers and foxes. As this description fits much of Europe, there is cause for concern.

The patterns of animal movement across a landscape are likely to predict the patterns of disease transmission (Albery et al. 2022). The usual range of disease transmission may be estimated using the home range size of an infected population, while dispersal distance could predict the maximum distance at which transmission may be considered a threat. Foxes tend to have large dispersal distances (21 km), while badgers in high-quality habitat may seldomly move beyond their neighbouring groups with a mean dispersal distance of 530 m (Macdonald et al. 2008, Walton et al. 2021). However, badger dispersal distances may substantially vary between different landscapes, as Byrne et al. (2014) demonstrates. Badgers in southwestern England had max dispersal distances as low as 1.7 km while Polish badgers dispersed as much as 17.5 km (Byrne et al. 2014). These differences in dispersal distance may reflect differences in the availability and distribution of quality habitat across the landscape. Badgers may also have more variable home ranges in lower density populations and in habitats which require more generalist foraging (Cresswell & Harris 1988). High-quality badger habitat may, therefore, lead to more localised disease transmission. The ineffectiveness of culls to reduce local fox densities suggests that foxes can disperse quickly and in substantial numbers, a trait which would make foxes especially suited to transmit disease to new areas (Baker & Harris 2006).

Wild boar also have home ranges that may vary in size according to resource availability, with larger home ranges occurring at higher altitudes (Fattebert et al. 2017). Dispersal distances in wild boar are moderate, with males dispersing significantly further than females (16 and 4.5 km, respectively; Truvé & Lemel 2003). Male wild boar may, therefore, be of greater concern for spreading *Mycobacterium bovis* far afield when compared to females. Fallow deer sexually segregate, the different sexes commonly occupying different areas across the seasons (Ciuti et al. 2004). Male fallow deer have larger home ranges than females (9.75 km^2 compared to 2.06 km^2) and travel furthest in the autumn (Borkowski & Pudełko 2007). Males tend to be displaced by females into lower quality habitats with more disturbance and higher predation risk, which might help explain why their home ranges are larger than females (Ciuti & Apollonio 2008). The sexual segregation of fallow deer might result in asymmetric disease prevalence within a population, with male deer at greater risk of infection and transmission. Since male fallow deer have larger home ranges and occupy more disturbed habitats than the females, it also seems probable that they would be more likely to encounter diseased animals and would be more likely to spread disease further afield. However, the smaller home range of female fallow deer is likely to result in higher population densities, making them more vulnerable to infection. The variation in home range size and dispersal distance seen in many of these species suggests that these factors cannot be thoroughly discussed without reference to the landscape and habitat quality. In some habitats, the threat of disease transmission may be very local, whereas upland or heavily forested

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landscapes seem likely to cause disease transmission to occur at larger spatial scales.

Summary of risk factors

All the species we examined utilise both woodland and open grassland habitats for resting or foraging, making it likely that they will occupy the same spaces in regions in which they co-occur (Escos & Alados 1992, Meia & Weber 1993, Virgos & Casanovas 1999, Morecroft et al. 2001, Cagnacci et al. 2004, Merli & Meriggi 2006, Plhal et al. 2014, Woodroffe et al. 2016). These species also co-occur in much of their range and with both fallow deer and boar populations expanding across Europe there is likely to be increasing geographic overlap between them in the future (Croft et al. 2019, Markov et al. 2022). Anticipating the expansion of wildlife populations is essential for developing effective management strategies for human-wildlife conflict, including wildlife disease (Barton et al. 2023). Given the spatial overlap of these species, indirect transmission of bovine tuberculosis between them is possible. Badgers, foxes and wild boar share similar nocturnal/crepuscular activity patterns, which increases their chances of encountering one another (Torretta et al. 2016, Ogurtsov et al. 2018, Rossa et al. 2021). Fallow deer are typically diurnal but may adapt their activity patterns in response to predation or human disturbance (Ciuti & Apollonio 2008, Caravaggi et al. 2018, Rossa et al. 2021). Since badgers, foxes and wild boar share similar habitats and activity patterns, direct transmission of the disease is a possible source of *Mycobacterium bovis* infection. The lack of shared activity patterns between fallow deer and the other species makes direct transmission between them less likely. However, the precise degree of temporal overlap between these species may be underestimated by comparing categorical estimates of activity. A more detailed comparison of temporal activity is needed to reveal the connectedness between these species.

Ingestion and inhalation seem to be the most common routes of infection, pointing to scavenging, infected food sources and shared airspace as the prime culprits of transmission (Gallagher & Clifton-Hadley 2000, Parra et al. 2006, García-Jiménez et al. 2013, Richomme et al. 2020). Shared airspace is probably a more common route of transmission between members of the same species than between species that are wary of each other since aerosols can only travel a few meters (Tang et al. 2006). The close associations of badgers and foxes may be the exception to this trend, especially when sharing a sett.

Food sources become contaminated through exposure to infectious materials. Although urine and faeces have been suspected as agents of infection, it seems unlikely these materials would be ingested in quantities sufficient for infection during foraging. A study in cattle found that faeces were avoided during grazing and this behaviour may also be found in other species (Smith et al. 2008). It seems more likely that shared food sources become contaminated via saliva or aerosol, especially at farms or supplementary feed sites. Saliva and aerosols are thought to contain higher numbers of CFUs than urine or faeces, and it seems likely that shared food sources would be ideal locations for the exchange of these infectious materials (Courcier et al. 2018). Maize and hay have both been shown to support *Mycobacterium bovis* for about a month in favourable conditions and supplementary feed sites have been connected to bovine tuberculosis transmission among deer in Michigan (Miller et al. 2003, Fine et al. 2011). Though infected feed sites may be a prime candidate for primary infection, there is likely another mechanism that facilitates disease transmission between species in the wild. The carcasses of animals in advanced stages of the disease may serve as hot spots of disease transmission. Carcasses of uninfected animals could also become contaminated through the saliva or aerosol of an infected scavenger. Many species in a wildlife community may engage in scavenging behaviour and hundreds of individuals may visit a single carcass (Häkkä Siviä 2021). Deer carcasses have been specifically noted as a common target of scavenging by wild boar, badgers and foxes (Kruuk & Parish 1981, Herrero et al. 2005, Webbon et al. 2006, Sidorovich et al. 2011). Given that three of the species often implicated with *Mycobacterium bovis* transmission are scavengers, the role of infected carcasses in disease transmission in the wild may be worth further examination.

CONCLUSIONS

Bovine tuberculosis in wildlife species has been widely researched, but many studies have focused on one species as the perpetrator of disease transmission. Our synthesis of the literature and analysis of *Mycobacterium bovis* infection prevalence revealed that single-species studies may miss important players in disease transmission. Future research should employ broader sampling campaigns and standardised *Mycobacterium bovis* sampling protocols to arrive at a clearer picture of bovine tuberculosis transmission in wildlife communities. A deeper understanding of wildlife community disease transmission would allow managers to better predict and control outbreaks of bovine tuberculosis, which would in turn enable a more efficient use of limited resources.

Though the precise mechanics of *Mycobacterium bovis* transmission between wildlife species remains unclear,

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scavenging and infected food sources seem likely candidates. More research should be conducted to quantify how these sites may drive the disease ecology of a wildlife community. Despite the limited data on *Mycobacterium bovis* infections in the wildlife community at large, badgers, fallow deer, wild boar and red foxes appear to be species of concern for the transmission of bovine tuberculosis between wildlife species. Significant behavioural overlap between these species may signify that a wildlife community is at high risk of *Mycobacterium bovis* infection should it be introduced to the area. The relationships between these species should be further explored to better elucidate the details of bovine tuberculosis transmission in a wildlife community – a feat which might be accomplished using modern bio-logging approaches and remotely activated cameras.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to report.

DATA AVAILABILITY STATEMENT

The authors have submitted the data used for this review as a supplemental file (Appendix S5) alongside the paper itself for the free use of any who should wish to use it. Inquiries regarding this data file may be directed to the corresponding author.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Details of the systematic searches.
Appendix S2. List of references included in the final analysis.
Appendix S3. All surveyed species with the count of surveys for each species.
Appendix S4. Distribution of publication dates for the papers used in the analysis.
Appendix S5. Raw prevalence data.

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