Annotated scientific bibliography relating to badger intervention and bovine tuberculosis for the period 1 January 2015 to 31 May 2024 (with later extension to 30 November 2024)

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Introduction

The purpose of this document is to provide a summary of the peer reviewed scientific literature published between 1 January 2015 and 31 May 2024 on findings on badgers and *Mycobacterium bovis* infection in relation to bovine tuberculosis (bTB) field intervention studies. The document provides a supplement, updating the scientific literature provided by the Tuberculosis Strategic Partnership Group (TBSPG) as supporting evidence for their recommendations in 2016. These articles have already been approved through each journals' peer review process, so no attempt has been made to critique these papers any further i.e. statements made in these papers are considered valid.

The methodology used in the selection of the peer reviewed papers included in this document is detailed in Annex 1 but in summary, terms relating to *M. bovis*/bTB, trial/intervention and badger were agreed. This search was then run on three literature specific databases (Web of Science, Scopus and MEDLINE). Each article derived from these searches was individually assessed for relevance (see Annex 1) and either included or excluded. A list of those articles selected for inclusion was then distributed to stakeholders to help identify any remaining gaps in the relevant peer reviewed literature published during this time interval. Only peer reviewed scientific articles (including reviews) were considered, and the agreed search terms used were:

(TITLE-ABS-KEY ("bovine tuberculosis" OR "bovine TB" OR "Mycobacterium bovis" OR "tuberculosis" OR "Mycobacterium tuberculosis complex" OR "MTBC") AND TITLE-ABS-KEY ("intervention*" OR "trial*" OR "vaccin*" OR "BCG" OR "cull*" OR "remov*" OR "control" OR "fertil*") AND TITLE-ABS-KEY ("badger*" OR "Meles meles").

This process provided a listing of 174 references to be incorporated into the annotated text. The text annotation of these references is to provide a high level, consolidated, factual, 'policy-neutral' statement of the scientific evidence produced from the selected peer reviewed papers with inclusion of occasional comments on the finding's context in relation to the Northern Ireland situation (subject to the resource and time restraint permitted). The narrative in no way replaces reading the articles directly (DOI links are provided with each of the references for this) as the following text only highlights the main points stated by the references.

The production of the following narrative required categorisation of the short-listed scientific articles into the following themes (with some articles cutting across multiple themes):

- Badger ecology
- Badger welfare & ethics
- Badger diagnostics
- Transmission dynamics
- Proactive badger culling
- Reactive badger culling
- Test and vaccinate or remove
- Badger vaccination

- Modelling
- Socio-economics
- Miscellaneous
- Future focus

Accurate reflection of some of the reported findings necessitated use of some technical/scientific terms and therefore a glossary of these terms and definitions is provided for convenience. For categories involving a longer narrative, an introduction including a brief explanation of the content is included along with a brief conclusion.

Badger ecology

Badgers are a widespread species in both the UK and Ireland and live in social groups in various types of habitats, preferring deciduous woodland in the vicinity of suitable pasture. They are primarily opportunistic foragers, although earthworms are considered the most important item in their diet. Badgers are a 'keystone' species in the UK and Ireland, i.e. a species that has a disproportionately large effect on its natural environment relative to its abundance, and one that plays a key role in maintaining the health and diversity of an ecosystem. Large scale population reductions may have an impact on established trophic webs.

The availability of suitable feeding resources and locations to dig setts (underground dens) are important factors in determining badger density and movements. In Northern Ireland there is an appreciable lack of woodland habitat and setts are often found in potentially sub optimal areas such as hedgerows or field boundary banks. Whilst bTB is a prevalent disease in species such as wild boar (*Sus scrofa*) and red deer (*Cervus elaphus*) in various European countries, the badger is considered to be the primary wildlife vector in the UK and Ireland (Reis et al 2021). There is therefore substantial interest in badger ecology owing to their involvement in the transmission of the disease to cattle (McClune et al 2015). The ranging behaviour of badgers, for feeding, mating, or dispersal reasons is of direct importance to the transmission of bTB infection both between individual badgers and between badgers and cattle (Gaughran et al 2019).

Population and abundance

Robust data on badger populations are a key component in assessing both conservation and management needs but present a challenge at large scale due to the badger's cryptic, nocturnal behaviour. Despite intensive study, there is still an element of uncertainty.

Population estimates in Northern Ireland over the period 1993-1994 to 2007-2008 suggested a relatively stable population with a best estimate of 34,100 (95% CI, 26,200 - 42,000) badgers (Reid et al 2012 referenced by Byrne et al 2021). This was hypothesised to be a result of either having reached carrying capacity or a depression of population growth via anthropogenic disturbance (e.g. road traffic collisions or sett disturbance) or disease. However, Byrne et al (2021) noted that the use of similar group size parameters between comparative datasets may cast doubt on the conclusion that the population has remained stable. In Ireland they determined that mean badger social group size may have been previously over-estimated, and that social group size varied with suitability of habitat to support badgers. The social group size of badgers was related to landscape type with areas with better feeding resources tended to have larger groups.

Comparative abundance estimates over a specified time frame are a central component in assessing the efficiency of control programmes. Minimum Number Alive (MNA) estimates are a widely used tool, but Ross et al (2022) suggest they are of limited use as either a badger population indicator or estimator unless in the context of long-term datasets. Whilst they acknowledged the potential value of MNA in enumeration studies they referenced certain subgroups, particularly younger or older individuals, that may be over- or under-represented in capture data. Additionally, individual ‘trap happy’ or ‘trap shy’ behaviours were considered a significant challenge and future development of a MNA modelling approach should ensure these factors are carefully considered.

Byrne and Do Lin San (2016) acknowledged biases in using MNA as an index of abundance. They recognised that there may be behavioural differences between badgers in areas subject to control pressures (through legal and illegal culling) compared to those in ‘uncontrolled’ areas, resulting in differences in respective survival ratios between these populations. Increased alertness and reduced trappability were likely factors in increasing survivability for badgers in control areas. They recommended alternative measures such as sett surveys to estimate trappability which could be used independently or along with MNA to remove potential biases.

Movements

Badger movements, particularly those beyond established social group territories, are relevant to disease-control interventions. Kelly et al (2020) examined both the reasons for, and the importance of, extra-territorial excursions (ETEs) in badgers. This Irish tracking study found excursions to occur throughout the year, with seasonal patterns present. Peaks in these excursions coincided with peaks of circulating sex hormones for both sexes, which from an evolutionary perspective is to be expected to permit outbreeding of social groups. The study suggested that ETEs of these Irish badgers were not motivated by food resources and are more likely to serve a monitoring role of neighbouring social groups. This may involve olfactory information from latrines, or actual contact with neighbouring badgers. Absence of either will indicate absence of territory owners and hence increase the probability of usage by neighbours. This highlights the potential role of perturbation and the need for scientific modelling to outline the necessary scale of badger intervention required to compensate for this effect and therefore achieve the desired disease control outcomes. The lack of ETEs undertaken by cubs is also referred to in the paper as making them a primary target for vaccination programmes before this behaviour exposes them to infection.

Byrne et al (2019) also considered factors likely to affect badger movements. Some, such as 'sex' and 'age', are well known to exert respective influences, whilst group composition and past-movement history have been less well studied. They acknowledged the potential failings in bTB management strategies of not incorporating the likely differences of badger movements in various landscapes.

Improvements in badger tracking technology may clarify how badger movements and interactions with habitat features relate to potential risks of disease transmission. Magowan et al (2022) compared GPS data with GPS-enhanced 'dead-reckoned' data, taken from two badgers tracked over a period of 14 days, and found that the latter provided greater estimates of distances travelled, (2.2 times longer), and confirmation of a higher proportion of time spent in the vicinity of hedgerows and field margins. Larger sample sizes would be required to permit population level comparisons, however this research could potentially enhance future modelling exercises aimed at predicting the spread of bTB.

Changes in badger behaviour as result of culling may also require the consideration of additional modelling parameters when attempting to estimate ongoing population changes (Byrne et al 2021). The movement of badgers from social groups on the edge of badger cull areas into newly vacated neighbouring territories may result in non-target population depletion that is difficult to incorporate into modelling studies (Byrne et al 2021).

Gaughran et al (2018) found that an average of 22% of male badgers were 'super rangers' travelling across various social group boundaries and maintaining this behaviour for extended timeframes (2-36 months). This was considered as being of particular importance in the potential spread of infection between social groups and therefore should be considered in epidemiological modelling and the formulation of disease control policy.

Benton et al (2016) showed that infection risks for badger cubs can be a function of kin-based association and therefore the perturbation of social and kinship structures should be considered during the design and delivery of disease management strategies.

Disturbance

Wright et al (2015) found that badger sett disturbance may contribute towards sustaining of bTB hotspots and therefore it has a detrimental effect on both cattle and badger welfare. Anthropogenic disturbance of ecosystems can have effects on spillover infection from wild populations to domestic animal hosts and is known to affect the socio-spatial structure of badger populations leading to the increased movement of animals amongst social groups (Byrne et al 2022a). Byrne et al (2022b) proposed the existence of density and age-dependant mechanisms affecting movement patterns in badgers within subpopulations. Their research found that older badgers and those living in higher densities or group sizes were less likely to move across putative territories. They suggested that culling in low density areas may have less of an effect on badger group social structure compared to high levels of badger removals in higher density populations, and therefore there may be relative differences in bTB prevalence and spread to non-culled badger populations. Importantly, they also referenced the differences in observed risk between Britain and the island of Ireland to cattle herds around targeted culling areas. The hypothetical impact of social perturbation on bTB prevalence in Britain does not appear to have been found in Ireland, although the respective use of cage traps in Britain and wire restraints in Ireland is likely to have caused various capture biases that do not permit direct comparisons.

The impact of large infrastructure developments such as road building schemes on badger movements requires further research. Barroso et al (2022), found that road construction was associated with an increased risk of bTB breakdowns in cattle within 1km of road construction in County Galway and considered badger perturbation as the most plausible explanation. However, Gaughran et al (2021) concluded that road construction did not cause badgers to change their ranging behaviour in ways likely to increase the spread of bTB. A GPS tracking study of badgers in Northern Ireland found that badgers generally avoid crossing dual carriageways and that major roads can be considered as strong borders for badger intervention areas (O'Hagan et al 2021a).

Research on the effects of tree felling operations on badger movements is inconclusive. Byrne et al (2022a), found mixed evidence of an association between bTB breakdown risk and the timing of clear felling activities in Ireland, for herds with farmsteads within 3 km. Leaving uncleared areas around badger setts may mitigate some of the potential disturbance effects of clear felling operations, however it may have less effect than comparative mitigation measures used for large roadbuilding projects which normally involve the use of badger-proof fences and underpasses.

Biosecurity

The implementation of biosecurity measures in and around farm holdings may significantly contribute to reducing the risk of bTB spread from badgers and improving human-wildlife coexistence.

Robertson et al (2019) reported on the different conclusions of previous studies in the UK and Ireland relating to badger activity levels around farmyards, with more recent studies reporting relatively little activity and a significant variation between individual farms. Their study, which used cameras to survey badger activity around 155 farms in the southwest of the UK, found that a significant proportion (40%) experienced badger visits to farm buildings. They suggested further development of a 'farm assessment tool' which used individual farm characteristics to produce a relative risk of the likelihood of badger visits with the potential to provide specific advice on farm biosecurity measures.

The intensification of agriculture over the last century means that the majority of land on which badgers prefer to forage for worms (grazed pasture) is within farm ownership and therefore knowledge of badger distribution is important for the management of bTB. At the farm level, typically the only information on badger activity available is from the farmers themselves. Robertson et al (2017) undertook a study comparing how well farmers estimates of the number of setts surrounding their farms correlated with field survey results and found only a 50% correlation. The same study also found that around 20% of farmers were unaware of badgers visiting their farm buildings. These findings are important when considering how they may inform management interventions that require trapping at setts or the avoidance of grazing within the vicinity of setts.

The locations of many badger setts on the island of Ireland relate to prevailing landscape features, particularly the lack of woodland, with the result that badgers often dig setts in hedgerows adjacent to grazing pasture. The proximity of badger setts to grazing cattle may be a contributing factor to the spread and maintenance of bTB in Ireland. Campbell et al (2020) looked at the importance of grazing management and its potential role in reducing the risk of bTB infection for cattle herds. They concluded that cattle stocked in fields containing setts and latrines may be exposed to a greater risk than cattle which are not stocked in fields with these features. They described grazing practices to help improve future biosecurity advice. These included fencing of setts, double fencing between neighbouring herds, or the avoidance of fields that contain setts for cattle intended for longer term housing.

Further considerations

Byrne et al (2024) summarised the advances that have evolved in badger bTB research on the island of Ireland during the period 2012-2022. They highlighted research gaps that if addressed should contribute to refining disease management strategies and informing national policies.

To date, badger population estimates at large scale have relied on identifying the types of setts in an area as a relative representation of the number of resident badger social groups. This is then multiplied by the mean group size to estimate overall abundance. The mean group size and territorial behaviours have since been shown to differ significantly between habitat types, an important consideration in assessing future abundance estimates. Future studies were advised to incorporate available technologies such as non-invasive hair sampling and genetic fingerprinting to increase the precision of population estimates (Byrne et al 2024).

GPS and proximity logging studies have provided data on badger movements in Ireland including those in and around cattle on both pasture and farmyards, as well as recording individual long-distance movements and differences in activity levels between seasons. The observed frequency of cattle visits to badger locations (e.g. setts and latrines) was more than three times higher than badger visits to cattle associated locations and therefore large-scale physical interventions such as the fencing of setts may have a role in reducing cattle bTB breakdown risk (Campbell et al 2019).

Repeated large-scale culling of badgers in Ireland reduced the risk of disease transmission to cattle herds within cull areas, but that this was never considered as a stand-alone sustainable option (Byrne et al 2024).

Badger vaccination was initially incorporated as part of the bTB control programme in Ireland in 2018/19 and has been expanded. It was also used in the Northern Ireland TVR research study. These studies have shown that knowledge of differences in population structure over time are important in ensuring that appropriate levels of vaccine coverage are achieved. Future analysis of existing datasets and the continued feedback between modelling and field data from future studies will also contribute to refining overall strategies (Byrne et al 2024).

Selective badger removal interventions and associated vaccination programmes rely heavily on trapping success to implement effective disease control strategies. Martin et al (2017) found that badger capture rates were highest in the vicinity of busy main setts and during wet weather conditions when the minimum temperature ranged between 3 and 8 °C. These were considered important parameters in optimizing the trapping and vaccine delivery success of future capture operations.

Rosen et al (2019) referenced the importance of badger reproduction data and the need for ongoing assessment if carcase availability is decreased by shifting to a vaccination programme. Population recruitment is likely to increase by shifting to vaccination and there remains a need to assess its influence on population dynamics and potential disease transmission. Increasing body weight was shown to be associated with an increased odds of pregnancy and therefore directly related to population growth. However, the exact reasons for premature cessation of lactation in Irish badgers, or an initial failure to conceive, requires further research. They suggested antemortem assessments of reproductive status including teat length comparisons and the use of ultrasonography.

Additional work on badger genetics (relating to the recent completion of the badger genome) opens the possibility of considering the implications of relative disease resistance among badgers. This may also have a direct bearing on transmission dynamics (which may vary between regions) and is therefore considered an essential future research goal (Byrne et al 2024).

Similarly, Conteddu et al (2024) aimed to identify knowledge gaps in peer reviewed literature that could provide insights to inform control policy for bTB and other zoonoses. There was a significant bias in the literature towards the badger-cattle episystem that predominates in north-eastern Europe. Only a small number of the 532 articles examined were found to have focused on management solutions and their efficacy or the effect of human wildlife disturbances on the spread of bTB involving wildlife hosts. The impact of roads, human perturbations, habitat change, and weather variables (particularly in relation to climate change) were also areas that received relatively little attention with most focusing on the effect of badger vaccination and culling on bTB dynamics. There was very little modelling of exit strategies.

The authors recommended future research to focus on generating high quality data on wildlife host distribution and abundance and linking this with mathematical and simulation modelling. The continued use and refinement of this modelling was considered a priority to assist policy makers (Conteddu et al 2024).

Conclusion

Robust badger population data are required to inform modelling of and progression of interventions. In general badgers remain within defined territorial boundaries. This behavioural characteristic may decrease the likelihood of bTB infection by neighbouring social groups or conversely increase infection and spread within a resident group, potentially exacerbated by anthropogenic disturbance. Badgers in Northern Ireland are likely to have a relatively higher numbers of setts in the immediate vicinity of grazing cattle. Biosecurity measures such as fencing off badger setts and latrines may make a significant contribution to reducing the risk of cattle infection by badgers.

The removal of badgers from an area has the potential to encourage ranging behaviour of neighbouring badgers into vacated territories which may increase the chances of spreading bTB.

Modelling exercises estimating badger populations should incorporate data on habitat variables and previous badger management in adjacent areas to ensure that the proposed scale of badger intervention will achieve the desired results rather than potentially exacerbate disease transmission.

Badger welfare & ethics

A limited number of papers address welfare and more particularly ethics in badger culling or other interventions in bTB control. All focus on badgers and only two referenced the island of Ireland in their considerations.

Welfare

Byrne et al (2015) assessed injuries in badgers captured by stopped cable restraint as part of badger culling in the Republic of Ireland. Over 18,500 badgers were assessed post-mortem, and no restraint-related deaths were reported. Eighty four percent of captured badgers showed no or minor injuries, although incidence of minor injuries increased with time highlighting the need for continual welfare vigilance. A number of seasonal and badger demographic variables were found to influence injury severity. In a study involving over 1,500 badger cage trapping events, 97% of badgers were reported as showing no signs of injuries (Menzies et al 2021).

McCulloch and Reiss (2017a) developed an Animal Welfare Impact Assessment tool (AWIA) in relation to bTB and badger control in England. They argued the need for an AWIA with equivalent mandatory standing to, e.g. Economic and Environmental Impact Assessments. Their tool was aimed at informing policy development, evaluating both positive and negative welfare impacts on both badgers and cattle. Direct welfare impacts to badgers from culling included lingering deaths, while indirect impacts were disruption of social groups, and disturbance. Their tool contains several assumptions and estimated that culling 85,000 badgers over a four-year period would result in 17,750 cattle not being slaughtered over a nine-year period. Similarly, an unspecified period of badger vaccination would result in 11,600 cattle not being slaughtered over a nine-year period.

McCulloch and Reiss (2017b) touched briefly on welfare, highlighting that badger anatomy and behaviour made free-shooting of animals problematic, with welfare issues for wounded animals.

Ethics

Garner (2017) examined the ethical implications of badger culling to address bTB from utilitarian societal betterment (the betterment of society as a whole), animal welfare and animal rights perspectives. He viewed utilitarianism as presenting difficulties in assessing total impacts and benefits - it neglected the impact on the individual and outcomes in bTB were uncertain. An animal welfare ethic justified the prioritization of human interests over animal interests, and Garner (2017) argued that in applying this, the killing of badgers should not be an ethical concern provided it was carried out humanely. He further argued that an animal welfare ethic was inadequate as it put exaggerated weighting on the importance of personhood (rationality, free will, self-consciousness), the justification for human moral superiority. He viewed according animals the protection of rights as an alternative to utilitarianism. This perspective dismissed badger culling as morally illegitimate. Different versions of animal rights (non-intervention, and intervention in certain circumstances) had a bearing on the use of badger vaccination, with Garner (2017) suggesting that even this may not be justified due to badgers' tolerance of bTB.

McCulloch and Reiss (2017c) took an animal rights-based approach to bTB and badger control, examining five Animal Rights theories. These theories grant sentient animals rights against being killed and/or caused to suffer by humans. The authors applied them to various badger interventions including culling and vaccination, and capture methodologies such as cage trapping. All assessed Animal Rights theories supported non-culling approaches to bTB, and the authors argued they actually went further in supporting a do-nothing approach instead of vaccination. This was based on (i) the primary justification for badger intervention being economic, (ii) bTB did not cause undue stress and suffering in badgers, whereas culling and vaccination did, and (iii) the scientific evidence suggested that bTB could be controlled by cattle measures alone.

McCulloch and Reiss (2017b) examined the interlinkages between science, policy and politics in badger culling in Great Britain. This paper provides a recent history of badger culling in Great Britain from primarily a political perspective and neatly summarises the underlying issue - 'That the badger has a role in the transmission of the disease to cattle is widely accepted. The nature of the disagreement revolves around two key questions. First, how much of a role does the badger play? Secondly, are there effective, practical and socially acceptable measures which can reduce the transmission?' The authors argue that policy should be informed not just by science, economics and public opinion, but also by ethics – the right or most justifiable policy.

McCulloch and Reiss (2017d) took a virtue-ethics approach to badger culling, looking at character traits ('virtues') including justice and proportionality, empathy and compassion. They argued that instead of a badger cull, a 'virtuous' government would focus on humane, and what they regarded as effective alternatives such as vaccination and stricter cattle controls. The paper calls for a rethink of animal health policies to align more closely with moral virtues that respect both human and animal interests. To that end the authors conclude with two recommendations: (i) mandatory Animal Welfare Impact Assessment to provide objective impact data, and (ii) robust ethical analysis of policy by independent experts.

McCulloch and Reiss (2018) proposed an independent UK Ethics Council for Animal Policy to address the moral aspects of issues such as badger culling, intensive farming and animals in circuses, something they identified as being missing in existing bodies. They proposed a six-stage analytical framework and argued a need for ethical expertise in policy making, citing models such as the Nuffield Council on Bioethics.

The above papers help inform a more holistic policy approach of the bTB/ badger problem, moving beyond traditional assessments of science and economics.

Badger diagnostics

This section outlines the main observations from papers mainly focusing on the diagnosis of *M. bovis* infection in badgers. As well as covering recent research relating to diagnostic tests (DPP test, IFNg test culture, PCR), this section also provides information on the negative welfare impact of capturing and testing badgers.

Thomas et al (2021) provided a systematic review of diagnostic tests used in wildlife, including badgers. They conclude that post-mortem examination and culture are useful methods for disease surveillance, but immunological diagnostic tests are becoming more important in wildlife bTB diagnosis. Serological tests are very useful given that they are relatively inexpensive and easy to perform and can be used in large-scale surveillance operations. This is further informed by more recent work validating the DPP test (a serological test; DPP = Dual Path Platform) for use in badgers (Arnold et al 2021, Ashford et al 2020, Courcier et al 2020). Research on direct detection of *M. bovis* from badger faeces through use of a PCR test (PCR =

Polymerase Chain Reaction) indicated good sensitivity (87.3-96.7%) and specificity (99-100%) against a panel of spiked samples. The authors suggest that this may be a tool that could be used in monitoring the impacts of bTB control measures (Murphy et al 2020).

Research into the use of the interferon gamma (IFNg) test has indicated that badgers with the highest IFNg values were most likely to subsequently test positive on both serological and culture tests, and this effect was detectable for 24 months after the IFNg test (Buzdugan et al 2017a, Tomlinson et al 2015). Sex and age had no influence on this result.

Further observations arising from the long-term data available from the Woodchester Park badger population concluded that recapture probabilities were higher in males, uninfected badgers and in captures carried out during the spring/summer period (Buzdugan et al 2017b). This may suggest that infection prevalence may be negatively biased if based on captured badger findings but may be advantageous with respect to vaccination efficacy given trapped badgers are less likely to be infected. Another analysis modelled the ability to detect an infected group of badgers based on 2 or more being positive to a test with a group size set at 15 (Buzdugan et al 2016). This required employment of two tests (Stat-Pak and IFNg tests) on each badger to accurately identify an infected group where 50% of the group were tested. Development of a test with a higher sensitivity (>80%) would help to decrease false positive rates. However, the smaller badger social group sizes encountered in Northern Ireland would make practical application of this technique unviable. Woodchester Park work has also indicated that fur-clips were only detectable for a relatively short period of time (several months) so were not suitable for marking vaccinated badgers longer term (Benton et al 2024).

Use of a physical restraint cage to facilitate collection of a small blood sample from conscious badgers has been shown to be relatively successful (Smith et al 2021). However, a negative impact evaluation on badger welfare was indicated for cage trapping, use of restraint cages or use of general anaesthesia for blood sampling with all of these processes being given intermediate welfare scores (never exceeding 5–6 out of a possible 8) (Colloff et al 2024).

Transmission dynamics

This section provides an update on recent findings relating to cattle/badger bTB transmission dynamics. A 2015 review (Gortázar et al 2015a) suggested a roadmap for furthering effective bTB control in wildlife. Issues relating to direct/indirect contact and environmental contamination are highlighted. The advances in *M. bovis* whole genomic sequencing (WGS) and its application to area-based studies are also presented. The review identified six research areas required to assist in effective bTB control in relation to wildlife:

1) a world map of bTB reservoirs and defined local bTB host demographics;
2) a more detailed understanding of the pathogenesis, epidemiology and behaviour of generalized diseased individuals;

3) a quantification of indirect bTB transmission within and between species;
4) harmonisation of wildlife disease monitoring protocols to enable bTB comparisons in both space and time;
5) carrying out controlled and replicated wildlife bTB control experiments using single intervention tools;
6) analysing cost-efficiency and consideration of knowledge transfer aspects in promising intervention strategies.

A 2016 review summarised the literature relating to the bTB risk factors for transmission to cattle (Broughan et al 2016a). Some risk factors are consistently identified (e.g. herd size, bTB history, presence of infected wildlife), but many risk factors are inter-related and many studies do not enable differentiation between cause and consequence of infection. The review suggests that the application of targeted, multifactorial disease control regimes that tackles the main risk factors simultaneously are likely to be a key to effective, evidence-informed control strategies. In Northern Ireland, similar risk factors to those identified by Broughan et al (2016a) were identified in chronic bTB herd breakdowns (Doyle et al 2020, Doyle et al 2022, Milne et al 2020). Similarly, in ROI, recurrence of infection through residual infection and local sources were considered key drivers of bTB (Houtsma et al 2018).

Downs et al (2022) developed a model for predicting areas where a badger reservoir was present using cattle surveillance data, but the model had low sensitivity (26-65%) and specificity (91%). A further development has been creation of a generalized model framework for individual badgers in Woodchester Park, which may be useful at looking at the behaviours of high-risk individuals (Konzen et al 2024).

Using an agent-based (*M. bovis*) model which focused on a localised area that utilised genetic and epidemiological data from cattle only, the preferred model required input from a hidden reservoir, which is postulated to be from badgers (O'Hare et al 2021). This hidden reservoir host was required to contribute to new local cattle infections within the model.

Direct/indirect contact

Infectious disease transmission requires direct or indirect contact between infectious animals and naive animals. Two systematic reviews looked at these contact definitions in relation to livestock and wildlife (Bacigalupo et al 2020, Ferriera et al 2023). A lack of consensus in these contact definitions was found with one review trying to develop a unified generic framework using a space and time combination (Bacigalupo et al 2020). The second review looked specifically at multi-host bTB scenarios (Ferriera et al 2023). Their review found that indirect interaction rates were 154 times higher than direct interaction rates and suggested that there should be a focus on preventing interactions in environments shared by different species. Studies on the island of Ireland have shown that indirect contact is more commonly observed and that badgers avoid accessing farmyards (Mullen et al 2015, Campbell et al 2019). An English study also found that badgers avoided direct contact with cattle, even though badgers preferred visiting land used for cattle pasture (Woodroffe et al 2016). Indirect contact between cattle and badgers using the same shared spaces over relatively short time intervals (less than 36 hours) was not uncommon with cattle visits being much more frequent that badger visits to these shared spaces (Campbell et al 2019, Woodroffe et al 2021).

Environmental contamination

Environmental shedding of *M. bovis* is required to enable indirect transmission. Jolma et al (2022) found that high DPP test readings (>100 optical density relative light units [RLU]) were associated with current *M. bovis* shedding in badgers but were not associated with future disease progression. Very high DPP test reading badgers (>1000 RLU) were four times less likely to be recaptured; possibly due to increased risk of enhanced mortality.

Chang et al (2023) developed a compartmental, environmental-transmission model using badger territories and cattle herd areas using data collected from the Kilkenny badger vaccination trial study (Gormley et al 2022). The model simplified transmission pathways (droplet, aerosol, faecal/oral) into one environmental transmission route and disentangles the quantitative relationship between relative badger density and local transmission risks. It suggests that use of badger vaccination can maximally reduce the average between herd R to 0.85 but that 30% of herds will still have a Reproductive (R) value >1. This model indicated that control is required across both cattle and badgers in this area. While this model implied that relative badger density was related to local transmission risks, a study in Northern Ireland did not find clear evidence of badger density contributing to prolonged bTB herd breakdowns (Milne et al 2020).

Whole-genome sequencing (WGS)

The ability to cost-effectively sequence whole genomes of *M. bovis* isolates combined with statistical, analytical software advances (e.g. Bayesian phylogenetic and machine-learning approaches) has enabled the exploration of transmission dynamics within areas to a more refined degree. Four studies targeted at different bTB hotspots across the UK and Ireland have yielded diverse results indicating that the transmission dynamics within different bTB hotspots can vary considerably. Indeed, some authors suggest that these divergent results are consistent with *M. bovis* transmission dynamics are likely to be context dependent, with the role of wildlife being difficult to generalize.

One study focused on the findings relating to Woodchester Park (Gloucestershire, England) and indicated that most transmission was in the intraspecies compartment, particularly cattle-cattle. While rarer signals of interspecies transmission were detectable, cattle were still at higher risk from other cattle. Badger-cattle transmission was ten-fold greater than cattle-badger transmission, but within-species transmission was much higher than inter-species transmission rates (Crispell et al

2019). A further study in England in an area where bTB was not a problem (Cumbria) indicated that the outbreak involved unwitting introduction of a *M. bovis* genotype only previously found in Northern Ireland, followed by transmission to multiple local cattle herds, spillover into local badgers, and spillback to cattle. It circulated in cattle for approximately six years before appearing in the badgers where it has continued to successfully circulate (Rossi et al 2022).

On the island of Ireland, analysis of WGS data from cattle and badger *M. bovis* isolates within the TVR project area indicated that cattle were likely driving the local epidemic. Most transmission was detected in the cattle-cattle compartment; badger-badger transmission was below detectable limits. Rare inter-species transmissions were detected, with models suggesting that transmission from cattle to badgers was more common than badger to cattle. Badgers appeared to be playing a smaller role in transmission of *M. bovis* infection in this study site, compared to cattle (Akhmetova et al 2023). However, the authors point out that this minor role involving badgers introducing infection may still be important for persistence if amplified by cattle-cattle transmission. Evidence of a multi-host *M. bovis* transmission system involving cattle, badgers and deer in Co. Wicklow has emerged (Crispell et al 2020, Kelly et al 2021). This is the first evidence of involvement of a third host within the UK and Ireland. Involvement of a third *M. bovis* host will further complicate attempts to eradicate bTB from cattle in such areas.

A review (Allen et al 2018) commented that badgers and cattle shared the same or highly similar pathogen sequence types consistent with frequent and recent transmission events, likely occurring in both directions. However, they hypothesised that the force of infection may be greater from badgers-to-cattle than cattle-to-badgers owing to the continual removal of infected cattle through test-and-slaughter with regional variations.

Duault et al (2024) suggested that an integrated approach and new outbreak reconstruction methods/transmission trees adapted to complex epidemiological systems and tested on realistic multi-host data may be needed to fully utilise the available data.

Conclusion

There is a lack of standardization/agreed definitions across studies to enable direct comparisons to be made, particularly in relation to indirect/direct contact rates and environmental contamination. This inhibits a fuller understanding of the cattle/badger/*M. bovis* interface. Insights provided through the application of WGS technology show that the relative contribution of the different species to the maintenance of *M. bovis* infection varies between bTB hotspots. However, to enable eradication of bTB in cattle within an area, the infection needs to be controlled in all *M. bovis* reservoir hosts connected to that area.

Proactive badger culling

This section looks at the peer reviewed literature on proactive badger culling in relation to the methodology, ecological effects and the variable results reported from different analyses of the data produced from proactive culling field trials. Proactive culling aims to reduce the force of infection of *M. bovis* in badgers through a large reduction of the population size through non-selective culling. This reduces badger density and therefore also *M. bovis* transmission rates.

Proactive culling methodology

The total eradication of a shared infectious agent is almost impossible if wildlife hosts, which serve as a natural reservoir of the pathogen are ignored. Eliminating or substantially reducing the number of abundant species can have indirect effects on other species. For instance, fox numbers increased after badger culling for bTB control in the UK. Culling can also have effects on the targeted species such as increased movement due to social disruption (dispersal and immigration). It has been suggested that the use of wildlife culls for disease control purposes should be proposed only when: (i) the pathogen transmission cycle is fully understood including all the host (vector) interactions; (ii) the response of wildlife populations to culling is known; and (iii) a cost-benefit analysis shows that increased revenue or benefit from reduced disease prevalence exceeds the cost of culling. In practice, random culling is seldom a stand-alone tool but rather one of several elements of an integrated disease control strategy, often based on vaccination (Gortazar et al 2015b).

Critical evaluation of the randomized badger culling trial (RBCT) revealed difficulties and limitations including the lack of a true ‘placebo’, the lack of repeatability, the enormous scale of the project, the intervention in a varied and complex landscape, the fact it had such a high public profile and the complexity of trying to understand the dynamic interactions of cattle, badgers, *M. bovis,* the environment and people. To combat these problems in future interventions mathematical modelling and cost benefit analyses may be useful along with the deliberate enrolment of multiple disciplines and the early awareness of the possibilities of perturbation (Cassidy 2015).

There have been discussions moving towards spatially targeted badger cull policies for bTB control. However, cattle bTB herd incidents were considered insufficiently clustered around bTB-infected badger setts to design an efficient spatially targeted badger cull based around infected cattle herds. Therefore, this is deemed not currently a viable option (Smith et al 2015).

Miguel et al (2020) outlines the practicalities of implementing a badger cull focusing on the importance of identification of the individuals to be culled as well as the spatial and temporal extent of the culling, the estimation of the population size, spatial distribution and connectivity of target species.

Ecology effects of pro-active culling

Culling was reported to be associated with a 61% increase (95% confidence interval [CI] 27%–103%) in monthly home range size, a 39% increase (95% CI 28%–51%) in nightly maximum distance from the sett, and a 17% increase (95% CI 11%–24%) in displacement between successive GPS-collar locations recorded at 20-min intervals. Despite travelling further, there was a 91.2 min (95% CI 67.1–115.3 min) reduction in the nightly activity time of individual badgers associated with culling. These changes were apparent while culls were ongoing and persisted after culling ended. The expanded badger ranging in culled areas was reported to be associated with individual badgers visiting 45% (95% CI 15%–80%) more fields each month, suggesting that surviving individuals have the opportunity to contact more cattle. Moreover, surviving badgers showed a 19.9-fold increase (95% CI 10.8–36.4-fold increase) in the odds of trespassing into neighbouring group territories, increasing opportunities for both badger-to-badger and badger-to-cattle transmission of *Mycobacterium bovis* (Ham et al 2019).

It was reported that if population reduction is too low, or too few groups are targeted by badger culling interventions, a ‘perturbation effect’ was observed, leading to increased movement and disease spread. Furthermore, successful control strategies could lead to increased disease if they are not implemented for long enough (Prentice et al 2019).

Evaluating the effect of badger culling on the presence of 55 bird species showed that 18 species showed significant or near-significant growth rate changes. Of these, four species had higher growth rates and 14 had lower growth rates in badger cull areas, compared to areas outside of the culling zones. Furthermore, 10 of 55 species showed significant or near-significant results, with only one species exhibiting a higher population growth rate in the presence of more intensive culling. Badger culling intervention did not predict whether the measured relationships were significant, or their directions, so there was little evidence to indicate consistent, community-level effects of badger removal on bird populations (Ward et al 2022).

Effect on bTB incidence

Lowering effect

Culling trials have demonstrated significant reduction in risk to cattle herds with this effect being larger in ROI than in (RBCT) trials in GB. In GB, badger culling was associated with a transient, increased risk also to herds found at the periphery of cull sites due to badger perturbation. However, this peripheral increased risk was transient (<2 years post-cull) and was not demonstrated during badger cull trials or government-led culling operations in ROI. The apparent beneficial effects of proactive culling to farms in cull areas have been maintained for up to 5–11 years after GB cull trials, and up to 10 years post-cull trial in ROI (Allen et al 2018).

The Badger Control Policy (BCP) was implemented in England for 4 years in 52 intervention areas (200–1600 km^2). The criteria for an area to be selected included:

being > 100 km^2, reasonable herd biosecurity measures, being within areas with high TB herd incidence, meeting minimum levels of participation, maintaining culling for at least 4 years, reducing badger population by at least 70% without eliminating any local populations, use of natural barriers at BCP boundaries (where possible), use interferon-gamma testing of cattle to supplement the usual tuberculin skin testing. The bTB herd incidence reduced by 56% (95% CI 41–69%) up to the fourth year of BCP interventions, with the largest drops in the second and third years. There was insufficient evidence to judge whether the incidence rate reduced further beyond 4 years. The authors of this study stated that this decline may be achieved by vaccination of badgers, fertility control and on farm biosecurity (Birch et al 2024) or some combination as it is very difficult to determine any cause and effect relationship when examining such field data.

Multivariable analysis showed that badger culling was associated with reductions in bTB herd incidence in the first 2 years in two intervention areas (Gloucester and Somerset) compared to areas without culling (incidence rate ratio (IRR): 0.79, 95% CI: 0.72–0.87, p < .001 and IRR: 0.42, 95% CI: 0.34–0.51, p < .001, respectively). An increase in bTB herd incidence was associated with culling in the 2-km buffer surrounding the Somerset intervention area (IRR: 1.38, 95% CI: 1.09–1.75, p = 0.008), but not in Gloucestershire (IRR: 0.91, 95% CI: 0.77–1.07, p = 0.243). Limitations of this study included the availability of only 2 years of data and the difficulty of determining the biological cause–effect relationship behind the statistical associations (Brunton et al 2017).

A study conducted in Ireland from 2009 to 2012 determined that repeated culling of badgers in high bTB prevalence cattle areas was associated with a statistically significant decreased prevalence of *M. bovis* infection in badgers (p < 0.001) following a longer temporal trend where unadjusted apparent prevalence declined from 26% to 11% during 2007 to mid-2011, followed by a stable trend between 9 and 11% thereafter up to 2013. Bovine TB prevalence in badgers appeared higher if caught at a sett, which was close to other infected setts. There was a positive association between badger bTB prevalence and cattle bTB prevalence within 1 km around setts (Byrne et al 2015).

A GB study determined that badger culling needs to take place for at least three years before any significant differences in the incidence of Official TB Freedom Withdrawn (OTFW) herd incidents are observed. In the RBCT there was a significantly decreased confirmed cattle bTB herd incidence within proactively culled areas and significantly increased confirmed cattle TB herd incidence up to 2 km outside the proactively culled areas. Thus, cattle bTB incidence should be monitored up to 2 km outside of culling areas (Donnelly et al 2015).

Pro-active badger culling in Gloucestershire and Somerset was associated with reductions in cattle TB herd incidence rates after four years but there were variations in effects between areas. Central zone incidence rates in Gloucestershire (Incidence rate ratio (IRR) 0.34 (95% CI 0.29-0.39, p < 0.001) and Somerset (IRR 0.63 (95% CI 0.58-0.69, p < 0.001) were lower with no difference in Dorset (IRR 1.10, 95% CI 0.96-1.27, p = 0.168) than comparison central zone rates. The buffer zone incidence rate was lower for Gloucestershire (IRR 0.64, 95% CI 0.58-0.70, $p < 0.001$), no different for Somerset (IRR 0.97, 95% CI 0.80-1.16, $p = 0.767$) and lower for Dorset (IRR 0.45, 95% CI 0.37-0.54, $p < 0.001$) than comparison buffer zone rates (Downs et al 2019).

Recently, Mills et al (2024a) re-evaluated the appropriateness of models used in previous RBCT analysis and found the frequentist and Bayesian models consistently showed beneficial effects within proactive cull areas with respect to confirmed bTB herd breakdowns. Similarly, Mills et al (2024b) re-evaluated the appropriateness of models used in previous RBCT analysis of zones neighbouring proactive cull areas and found there was an adverse effect during the culling period on confirmed bTB herd breakdowns but a negligible effect when culling was stopped. These results are consistent with the original peer reviewed findings but differ from the analytical findings reports by others who reported no effect from the RBCT data, particularly if all (confirmed and unconfirmed) bTB herd breakdowns were considered (Langton et al 2022, Torgerson et al 2024).

No effect

Government (Defra) data obtained from England's High Risk Area over a long time period (2009-2020) within and outside of culling areas were analysed. Herd incidence and prevalence trends were followed and a range of mathematical models were applied to the available data. These analyses failed to identify a meaningful effect of badger culling on confirmed bTB breakdowns in English cattle herds (Langton et al 2022). Heavily culled counties had similar disease reduction patterns to lightly culled counties, with peaks at or before 2015 and reductions thereafter suggesting that factors other than badger culling are influencing bTB herd incidence in cattle. There have been similar modest improvements in bTB incidence across both culled and unculled areas of the HRA since 2015. Cattle related measures were implemented alongside culling badgers and the authors attributed these cattle-based measures as the most likely explanation for the changes over time. Furthermore, the authors state that during the same period (2009–2020), Wales achieved similar reductions in herd bTB incidence as England through the introduction of improved bTB testing and other cattle measures, and without widespread badger culling (Langton et al 2022).

Further analysis applied various statistical models to the RBCT data indicated that the result obtained depended on the model applied (Torgerson et al 2024). It was noted that no models showed an intervention effect when all bTB herd breakdowns were considered (cf. confirmed bTB herd breakdowns).

Pro-active culling vs reactive culling and vaccination

Random and selective culling strategies are more likely to succeed in isolated populations than on large geographical scales, and the results will probably consist of a certain reduction of disease prevalence in the wildlife host and in the domestic host targeted, rather than in the total eradication of the infectious agent. Taking no action to control diseases can result in higher costs. One example is the dramatic increase in prevalence of bTB in badgers after the suspension of TB cattle testing during the FMD epidemic in the UK in 2000–2001. This was ascribed to the high prevalence of cattle herd infection and cattle with advanced disease (Gortazar et al 2015b).

Conclusion

In relation to pro-active culling, it is worthwhile to note the need for meticulous planning in relation to the spatial and temporal extent of the culling, the estimation of the population size, spatial distribution and connectivity of target species. The potential effect of a proactive culling strategy on badger behaviour, such as increased ranging distance, also needs to be taken into account. The majority of previous studies have reported beneficial effects of culling strategies in both badger populations and cattle herds. However, it needs to be noted that culling strategies in general were rolled out alongside enhanced cattle-based measures.

Reactive badger culling

Reactive badger culling involves the non-selective removal of badgers from a limited area around an bTB infected herd (Bielby et al 2016). The method has been employed for many years in ROI with up to 30% of the agricultural land being subjected to this intervention. This has led to many of these reactive culls coalescing into larger areas. Reactive badger culling was also investigated during the RBCT in England, although terminated prematurely when cattle TB incidence increased in buffer zones.

Intermediate reductions in badger density, as achieved by localised reactive culling in the RBCT, significantly increased cattle bTB (Bielby et al 2016). The spatial scale over which localised badger culling had its biggest impact was investigated. Reactive badger culling had a significant positive association with the risk of cattle bTB at distances of 1-3km and 3-5km, and no such association existed over shorter distances (<1km). These findings indicate that localised badger culls had significant negative effects, not on the land on which culling took place, but on adjoining lands and farms (Bielby et al 2016).

During 2014, a substantial area-level bTB outbreak developed in north County Sligo, necessitating an enhanced response. Prior to 2014, badgers were removed at a low intensity in the study area under licence as part of a national bTB control strategy. Subsequently, many of the restricted herds qualified for badger removal in their vicinity as part of the enhanced response. Reactive culling was applied to assist bringing the outbreaks under control. No definitive source was identified, nor reasons why a substantial number of herds were infected over a relatively short period (Doyle et al 2018).

Smith et al (2022a) recommended that before any localized wildlife intervention starts, four initial considerations need to be made: Confirm, Clarify, Resource and Exit. That is, (a) confirm that wildlife species are likely to constitute maintenance hosts, (b) clarify the overall objective (disease elimination, containment or mitigation), (c) ensure sufficient resources are available to achieve the desired goal and (d) identify the exit requirements for disease elimination. The suggested steps involved included: initial surveillance, defining the minimum infected area by producing a single contiguous area containing badger territories of bTB confirmed badgers overlapping high- and medium-risk farmland, buffering the minimum infected area, defining the method of control, implementing control, measurement and adaptation when required (Smith et al 2022a). Further practical guidance on instigating a regional multi-species control approach were detailed by Tratalos et al (2024); in determining boundaries, knowledge of the ecology, habitat, population densities, and natural routes and boundaries to migration for the species of concern (badgers or cattle) are all important.

Conclusion
Trials into reactive localised culling have shown significant negative effects, not on the land on which culling took place, but on adjoining lands and farms. However, irrespective of the method being used in a trial, thorough preparation, sound methodologies and sufficient resources are paramount.

Test and Vaccinate or Remove (TVR)

In this section, a summary is provided on the key findings from the badger TVR study undertaken in Northern Ireland. Apart from modelling outputs, no other such studies have been undertaken although a TVR approach has begun in France (Boschiroli 2023).

A selective badger cull combined with vaccination approach, commonly referred to as a test and vaccinate or remove (TVR) strategy, was undertaken in a 100km^2 area of Northern Ireland (2014-2018). The area was chosen as it had a high cattle herd density and badger density as well as having a high bTB prevalence relative to the rest of NI. The methodology and protocols used (Menzies et al 2021) provided valuable information on the logistics and resources required for such a badger intervention strategy. This study demonstrated that trap-side testing of badgers was a viable option and it assisted in validating the DPP test (Arnold et al 2021, Ashford et al 2020, Courcier et al 2020, Menzies et al 2021). The DPP test characteristics using whole blood showed a sensitivity of 69% (95% credibility interval [CrI]: 48%–88%) and a specificity of 98% (95% CrI: 96%–99%). Furthermore, TVR in this area did not appear to affect the size of the badger population nor cause any increased movement of badgers with the social group structures seemingly remaining undisturbed (Allen et al 2022, O'Hagan et al 2021, Menzies et al 2021, Redpath et al 2023).

The TVR study did show a significant downward trend in the annual badger *M. bovis* prevalence from 14% (95% CrI: 10%–20%) to 1.9% (95% CrI: 0.8–3.8); a 39.1% annual reduction in prevalence (95% CrI: 26.5–50.9) (Arnold et al 2021). However, TVR had no obvious impact on cattle herd bTB levels; it was shown that cattle-to-cattle transmission was the main driver of *M. bovis* infection in this area (Akhmetova et al 2023, Doyle et al 2023).

As previously mentioned, a four-year pilot TVR intervention study started in France in 2023 (Boschiroli 2023).

Conclusion

The TVR project demonstrated that trap side testing of badgers was a practical, real-time decision tool using whole blood DPP testing. The significant year-on-year decrease in badger DPP test positivity needs to be considered along with the design deficiencies of lack of replicate and control areas. However, its legacy of a vaccinated badger population, along with no signs of increased badger perturbation is an advance when moving forward to a vaccination only control measure. The results do suggest that there is a need for enhanced cattle bTB control measures alongside an area-based badger intervention.

Badger vaccination

Context

Vaccination of badgers, most likely with Bacillus Calmette-Guérin (BCG), has been proposed as a method to potentially reduce bTB transmission within the cattle-badger multi-host system that exists in the UK and Ireland. A considerable amount of lab-based, experimental, and field-based research has been undertaken in recent decades and has already been considered in detail by the Tuberculosis Strategic Partnership Group (TBSPG) when making their previous recommendations in 2016.

To recapitulate briefly, pre-2016, an injectable BCG vaccine for badgers was available from DEFRA, had been licensed and was in field use in several relatively large badger vaccination demonstration projects, and many smaller projects, in Ireland and GB. A BCG version, formulated for oral administration, was also being trialled. There had been no large-scale trials of the impact of badger vaccination on disease risk in cattle comparable to the RBCT; consequently, results were eagerly anticipated.

The supporting science consensus was that, although BCG vaccination did not generate complete protection or sterile immunity, it could reduce host susceptibility. BCG vaccination in badgers reduced disease severity and progression following challenge infection with *M. bovis*; the risk of BCG vaccinated badgers testing positive (seroconverting) was reduced by 74% (the risk of testing positive to any of the live tests of infection was reduced by 54%) in a relatively small GB trial (Carter et al 2012, reviewed by Godfray et al 2013). There was no evidence that badger BCG vaccination significantly changed the ranging behaviour of badgers (Woodroffe et al 2017). However, badger vaccination was likely to have little if any effect on the course of pre-existing *M. bovis* infections (Robinson et al 2012). The risk of infection of unvaccinated cubs in a vaccinated social group was reduced by 79% when more than a third of the social group was vaccinated, probably due to reduced infectiousness of vaccinated badgers (Carter et al 2012). Given the uncertainty over the duration of vaccine-induced immunity in badgers and the need to inoculate new cubs, repeated annual vaccinations were thought necessary (Godfray et al 2013, Godfray et al 2018).

In Ireland, between 2009 to 2012, “the Kilkenny field trial” investigated the effect of badger BCG vaccination on bTB incidence within a natural badger population where reactive culling had been taking place for several years (Gormley et al 2017). BCG vaccination was estimated to reduce badger susceptibility by 59%. Modelling these parameters estimated that the disease could be eliminated over time with ≥30% vaccination coverage, provided current cattle and wildlife controls were retained (Aznar et al 2018). However, the model assumed no cattle-badger or environmental transmission component and assumed homogeneity across the landscape, resulting in uncertainty about the effectiveness of badger BCG vaccination intervention and its impact on local transmission dynamics. This remains the subject of ongoing research (Ryan et al 2023), including advanced mathematical models to evaluate potential interventions, which suggest that host densities are important drivers (Chang et al 2023).

From 2018, routine badger BCG vaccination has been established within the Irish bTB eradication programme, replacing reactive culling across >20,000 km^2; >6,500 badgers were captured in vaccination areas in 2021 and >5,800 in culling areas (Ryan et al 2023). Assessing the impact of this intervention requires information on vaccine efficacy and vaccination coverage, which is accepted as logistically challenging. These data are being analysed currently (Ryan et al 2023).

The following narrative synthesizes relevant findings from 37 peer-reviewed studies 2016-2024, inclusive, shortlisted from a literature review and provides a policy-neutral review of the natural science evidence base, including insights into vaccine efficacy and safety, deployment strategies, behaviours and attitudes, and the challenges faced in badger vaccination programmes.

General findings

Buddle et al (2018) reviewed the efficacy and safety of BCG vaccine for controlling bTB in livestock and wildlife. Protection was observed against severe generalized bTB but was not complete; vaccinated animals still harboured *M. bovis* in bronchial lymph nodes. BCG vaccination in badgers reduced disease severity and bacterial load; both oral and intramuscular routes were effective. Studies across various species indicated that BCG vaccination was safe, with no severe adverse reactions reported (Bianco et al 2020). BCG-induced protection varies, based on factors such as vaccination route, dose, and environmental exposures; high oral doses were required for effective protection, whereas routes other than oral or intestinal were generally more effective. Neonatal vaccination provided better protection; revaccination strategies need optimization. Field trials confirmed the potential of BCG to reduce infection rates and disease severity in cattle and wildlife under natural conditions. The duration of protection varied, with immunity waning after 1-2 years.

Balseiro et al (2020a) also reviewed the current state and challenges in the development of bTB vaccines for animals. The BCG vaccine, developed in the early 20th century, remains the only vaccine available for TB and has been extensively used in humans and experimentally in animals. Live BCG vaccines have been evaluated in numerous studies and demonstrate varying levels of protection across species such as cattle, goats, sheep, wild boar, deer, and badgers (Robinson et al 2012). Heat-inactivated (dead) *M. bovis* (HIMB) vaccines may be alternatives to (live) BCG, showing some promise in small scale wild boar and badger studies (Balseiro et al 2020). BCG vaccinations reduce bTB severity but do not completely prevent infection; HIMB vaccines show only partial efficacy (Balseiro et al 2020b). Delivery of wildlife vaccination, such as via oral baits, poses significant logistical challenges but may, in the future, offer practical solutions for some larger-scale vaccination efforts (Balseiro et al 2020b).

Experimental vaccine challenge

Before randomised control field trials could even be considered, BCG and various candidate vaccines were required to be tested experimentally in captive badgers under controlled conditions. Chambers et al (2017) evaluated the efficacy of oral formulated BCG vaccination in reducing bTB development in experimentally infected captive badgers. Vaccination generally reduced the dissemination of *M. bovis* beyond the thorax. *M. bovis* was isolated intermittently from clinical samples post-challenge but not from faeces. It was stated that the challenge model's high *M. bovis* dose may exceed natural exposure levels, impacting vaccine efficacy assessment. Low excretion rates suggested minimal environmental contamination risk, supporting the safety profile of oral BCG. Further research was advocated to determine the optimal oral BCG dose for effective bTB control in wild badgers.

Perrett et al (2018) evaluated the safety of administering BCG vaccine orally to badgers to determine if adverse effects followed the oral administration of the BCG vaccine, to measure the quantity and frequency of BCG excreted in the faeces of vaccinated badgers, and to assess whether there was any evidence of the vaccine spreading to unvaccinated, 'sentinel' badgers sharing the same environment. BCG was cultured from faecal samples in 3 of 9 vaccinated badgers; no BCG was detected in laryngeal swabs, tracheal aspirates, or tissues collected post-mortem; no BCG transmission to sentinel badgers was detected. The risk of oral BCG affecting non-target species, including cattle, seemed relatively low, particularly with controlled bait deployment protocols to minimize access by non-target species (Perrett et al 2018).

Vaccine field trials and deployment

While experimental studies pre-2016 suggested that BCG vaccination would reduce bTB susceptibility in badgers, systematic field trial data were largely missing. Gormley et al (2017) investigated whether direct oral administration of BCG vaccine protected free-living badgers against natural *M. bovis* infection. The “Kilkenny trial” was conducted over three years across >750 km² divided into three zones with different treatments i.e. vaccine/placebo coverage and no hard borders; time to seroconversion was the primary outcome, supplemented by postmortem examinations. The area had been subjected to badger culling for several years prior to this trial. The study demonstrated that oral BCG vaccination significantly delayed the time to seroconversion, indicating some protection against bTB. The increase in vaccine efficacy related to reduced susceptibility with higher vaccination coverage suggests a positive impact on herd immunity. This initial study did not measure the direct impact on cattle bTB rates.

Further analyses (Gormley et al 2022) of the Kilkenny trial data confirmed the initial findings (Gormley et al 2017). Infection prevalence was significantly lower in vaccinated (24%) compared to placebo (52%); no significant differences were observed in the number of infected sites or severity scores between vaccinated and placebo-treated badgers across zones. Notably, no infection was detected in non-treated badgers, suggesting an indirect protective effect from the vaccinated population, and suggesting that vaccination primarily reduced susceptibility, rather than altering disease progression in infected individuals.

Mathematical models (Aznar et al 2018), based on Kilkenny trial data, estimated the vaccine efficacy measure for "susceptibility" to be 59%, indicating a significant reduction in susceptibility to *M. bovis* infection among vaccinated badgers. However, the efficacy measure for "infectivity" suggested no significant reduction in the infectiousness of vaccinated badgers that became infected. Further analyses of the basic reproduction (R) number suggested that eradication of *M. bovis* would be feasible with a vaccination coverage ≥30% if current cattle and badger control measures remain; timescale was probably decades.

Ireland investigated the effect of badger BCG vaccination on bTB rates in cattle herds in a relatively large field trial and produced further context-dependent evidence that badger vaccination, in a previously reactively culled badger population, can be "no worse than" ongoing targeted (reactive) culling. Using a specialised study design (non-inferiority trial), Martin et al (2020) compared targeted badger culling with BCG vaccination in seven counties in Ireland from 2011 to 2017; the outcome of interest was incidence of new bTB cattle herd breakdowns. Despite significant variation in the effect of badger vaccination across study sites, the study demonstrated that badger BCG vaccination was not inferior to (i.e. no worse than) targeted culling in reducing bTB incidence in cattle herds in most, but not all, study sites. Although variability across study sites may limit generalizability, the study concluded that badger BCG vaccination was a viable alternative to ongoing targeted culling for bTB control in cattle herds in Ireland. This study, which informed the subsequent 2021 Irish bTB eradication strategy, was discussed by Ryan et al (2023); a large-scale vaccination programme for badgers using BCG has now been rolled out over 20,000 km². Analyses are ongoing to determine the actual effectiveness of this intervention, which is influenced by vaccine coverage logistics and vaccine efficacy (More et al 2019).

In GB, Benton et al (2020) evaluated progress, operational effectiveness, and motivations behind badger vaccination programmes in England. Key barriers included funding, low confidence in vaccination among farmers, and logistical challenges, including vaccine supply. Vaccine coverage was consistent with modelled requirements for disease control, supporting the feasibility of vaccination as an option to support bTB management; data on vaccine efficacy were not reported. Further analyses (Benton et al 2023) assessed the effort required to vaccinate badger populations following culling operations, which is important as the

Government's strategy pivots towards vaccination. Achieving high vaccine coverage in post-cull populations may require more trapping nights and careful planning. Vaccination logistics are challenging to maintain; decline in trapping efficiency over successive culls suggests that badgers become wary and increasingly difficult to capture, consistent with previous research, with lower efficiency in the autumn. The impact of these badger vaccination operations on bTB prevalence in local cattle herds was not assessed.

A 4-year vaccination campaign was undertaken in a small area (11km^2) of Cornwall (Woodroffe et al 2024). The vaccination coverage was estimated at 74% (95% CI: 40-137%) along with an indication of a fall in *M. bovis* test-positive badgers over time. However, the vaccination area was in proximity to an active cull area, which may confound interpretation of these findings.

Vaccine-related badger pathogenesis and immunology

Birch et al (2021) developed the Disease Burden Score (DBS) for assessing the severity of bTB lesions in experimentally infected badgers to improve the consistency and precision of bTB vaccine efficacy studies. DBS provides a robust and unbiased measure of disease, facilitating more accurate comparisons of vaccine efficacy across different experimental studies. Potential immunological contributors to badger susceptibility to *M. bovis* have been investigated (Bilham et al 2017).

Boggiatto et al (2023) provided a comprehensive review from multiple studies on the immune responses to *M. bovis* infection and BCG vaccination in various wildlife species, including badgers. BCG vaccination reduces disease severity, characterized by fewer lesions, limited dissemination, and reduced bacterial loads. Potential vaccination routes were discussed; there is more evidence regarding intramuscular or oral administration. Bait formulation for oral delivery requires further research. Targeted vaccination in high-prevalence areas may be more feasible and cost-effective than mass vaccination.

Vaccine reagents

The approved badger vaccine (BadgerBCG) is derived from the *M. bovis* BCG Copenhagen 1331 variant. However, due to a global shortage of BCG for human use, other variants were considered. Courcier et al (2022) investigated the effects of different BCG strains and the impact of repeat vaccinations on the efficacy and specificity of animal-side immunodiagnostic tests for *M. bovis* infection in badgers. This field study was undertaken within a larger wildlife intervention project (TVR: as previously described). The study demonstrated that BCG Sofia induces a significant serological response to one of the test antigens (MPB83), complicating the use of the animal-side test (DPP VetTB assay) shortly after vaccination. BadgerBCG did not significantly affect DPP VetTB assay results, making it a more suitable option for vaccination programmes.

McGill et al (2022) investigated the immune responses in badgers vaccinated with multiple doses of BCG Sofia, focusing on the antigen MPB83. Although BCG Sofia induced a robust immune response in badgers, vaccination with BCG Sofia could result in detectable serological responses against MPB83, potentially compromising the diagnostic performance of assays targeting this antigen. The study suggests that repeated vaccination with BCG Sofia could interfere with serological diagnostics.

Vaccine candidates for badgers, other than live BCG, continue to be developed and assessed. One such is heat-inactivated *M. bovis* (HIMB, Juste et al 2023). This laboratory trial with captive badgers assessed various clinical, immunological, pathological, and bacteriological parameters to determine vaccine protective efficacy. The HIMB vaccine provided partial protection, as indicated by reduced lesion severity and bacterial load in the standard vaccinated group compared to controls.

To potentially improve the vaccine supply chain, the efficacy of an oral bioreactor-grown BCG vaccine was evaluated (Lesellier et al 2020). The study focused on comparing direct oral administration of BCG with vaccine delivery through bait consumption to determine the feasibility and effectiveness of baited vaccine delivery. Manually administered BCG demonstrated consistent and significant protection against bTB challenge, as evidenced by reduced DBS (Birch et al 2021) and robust immune responses. Bait administered BCG showed variable protection with no significant group-level effect. Manual vaccination shows promise for controlled environments but may be challenging to scale; baited delivery, while promising, required further refinement to ensure consistent protection.

Vaccine delivery routes

Informed by the costs and logistics of badger trapping from various field trials in the UK and Ireland, delivery of a vaccine to wildlife in bait form has been the subject of substantial research. Pre-2016, reagents and evidence from trials were insufficient to inform a decision to deploy.

Gowtage et al (2017) developed a palatable bait and compatible vaccine carrier for oral delivery of BCG vaccine to badgers and assessed bait palatability, physical properties, microbiological safety, and vaccine stability within the bait under various storage conditions. This laboratory and field trial involved captive and wild badgers and included multiple batches of bait tested over two years, involving both captive and field conditions. Study findings support the potential for using baits for the oral vaccination of badgers in field conditions, pending further efficacy testing; the study focussed on bait uptake, rather than providing new evidence on vaccine efficacy.

Carter et al (2018) investigated the optimal strategy for maximizing the uptake of a mock oral vaccine by wild badgers using bait. This field study involved 40 badger social groups across three regions in southwest England (>800 km^2). Marked baits (not containing vaccine), composed of peanuts and syrup, were deployed at badger setts either in late spring or summer, above or below ground at sett entrances. This study demonstrated that high levels of bait uptake could be achieved in wild badger populations using a palatable bait deployed in the springtime. The findings support the development of effective oral vaccination strategies by highlighting the importance of comprehensive baiting at both main and outlier setts and considering seasonal variations. The simplicity of placing bait at sett entrances without significant loss in uptake efficiency offers a practical approach to larger-scale vaccination efforts. The study focussed on bait uptake, rather than providing new evidence on vaccine efficacy in badgers or cattle.

Lesellier et al (2019) investigated uptake and persistence of BCG vaccine in badger tissues following two direct vaccination routes (oropharyngeal instillation and direct delivery to the small intestine/ileum) using trapped badgers, to determine the ability of these routes to deliver live BCG and induce an immune response. Badgers showed no significant adverse effects from vaccination; no live BCG was detected in faeces, although BCG DNA was found, indicating some level of faecal excretion without confirmed bacterial viability. The oropharyngeal instillation route showed better BCG persistence and immune response induction, suggesting it may be more effective for oral vaccination in badgers. The tonsils and draining lymph nodes were primary sites for BCG uptake and persistence. The study concludes that oropharyngeal instillation of BCG provided better persistence and immune response compared to ileal/small intestine delivery in badgers.

Palphramand et al (2017) evaluated field performance of various bait formulations designed to deliver the BCG vaccine orally to wild badger populations in Woodchester Park, Gloucestershire, UK. The study identified an attractive and palatable bait and vaccine carrier combination suitable for further development for oral delivery of the BCG vaccine to wild badgers. The study provided no evidence on vaccine efficacy in badgers.

Further badger bait delivery studies in France (Payne et al 2022) demonstrated that oral vaccination using baits can potentially achieve a substantial uptake in wild badger populations. The combination of biomarker detection and genetic typing provided a robust method for estimating bait uptake non-invasively. The study demonstrated the feasibility of using non-invasive methods to estimate bait uptake by European badgers in a bTB-infected area.

Oral vaccination and non-target species

There was concern about bait-delivered BCG vaccine being taken up by non-target species, including cattle, where non-specific test cross reactions might become problematic. There was also likely to be significant and uncontrollable variability in bait uptake by badgers; some were likely overdosed, while some took no bait (Robinson et al 2012).

Robertson et al (2015) investigated the extent to which non-target wildlife encountered vaccine baits intended for badgers. Small rodents and rabbits were the primary species interacting with baits. Baits placed down sett entrances were primarily taken by small rodents. Squirrels and rabbits were also significant in their interactions with baits, particularly those placed under tiles. The findings highlight the need for targeted bait deployment strategies to minimize non-target uptake and ensure effective vaccination coverage for badgers.

Further work (Robertson et al 2016) investigated badger behaviour and non-target wildlife species towards three candidate baits designed for oral delivery. No significant preference for any bait type was observed among badgers. Factors influencing the uptake of oral vaccine baits by badgers were determined (Robertson et al 2022). Higher bait quantities increased uptake among cubs but not adults; uptake was positively associated with higher badger activity at setts. Deploying baits directly into sett entrances significantly increased bait uptake compared to placement under tiles.

While the prospects for bait delivered vaccine remain attractive, the inherent variability, uptake by (and potentially passive transfer from) non-target species, and other well documented logistical difficulties informed a decision not to proceed further with this oral bait approach, at least in Ireland (Ryan et al 2023); injectable/oral BCG remains the leading candidate for badger vaccination.

Vaccine models and badger population estimation

Schreiner et al (2020) found that vaccination campaigns, timed immediately after the birthing season, best protect the population by targeting the peak influx of susceptible newborns. Their bTB badger model suggested that, due to the longer life span and low virulence of bTB in badgers, timing of vaccination had a lesser impact on immediate outcomes. However, vaccination at or before the end of the birthing season still provided better control over the pathogen.

Smith et al (2020) estimated badger vaccination coverage by live-trapping and injecting with BCG within a bTB control initiative in Wales (Intensive Action Area; 'IAA' Wales). The study demonstrated that genetic methods could effectively estimate vaccine coverage in wild badger populations. The study accounted for potential sources of error, enhancing the reliability of the estimates.

Simulation mathematical modelling was used to investigate the effects of partial BCG vaccine protection on bTB in badgers, to understand potential long-term effects of repeated vaccination campaigns on disease prevalence in badgers, and to explore whether partial protection could still contribute to disease eradication (Smith et al 2022b). Various scenarios were tested, including different probabilities of full, partial, and no protection; simulations were run for 5, 10, and 50 years of vaccination followed by periods with no vaccination to assess long-term impacts. While the model did not appear to account for external infection pressures, such as immigration of infected badgers or cattle-to-badger transmission, the study provided useful insights into the potential of BCG vaccination to control and eradicate bTB in badger populations. Findings suggest that even with partial protection, badger vaccination can significantly reduce disease prevalence and contribute to eradication efforts.

Badger behaviour related to vaccination

Woodroffe et al (2017) investigated whether BCG vaccination, or the process of live trapping to administer the vaccine, affected the ranging behaviour of badgers to address concerns that vaccination, like culling, might inadvertently alter badger ranging behaviour and potentially increase the risk posed to cattle. Vaccination was shown to have no significant effect on monthly home range size; mean home range sizes were similar between vaccinated and unvaccinated badgers; no significant changes were observed in badgers tracked before or after vaccination. Culling significantly increased badger home range size, whereas vaccination did not; proactive culling increased home range by 180%, reactive culling by 74%, compared to no significant increase with vaccination. The study showed that BCG vaccination was unlikely to cause adverse behavioural changes in badgers, unlike culling.

Vaccine related farmer behavioural science

A substantial amount of behavioural or social science research has been undertaken to understand stakeholder views on controlling the cattle-badger interface, including badger vaccination.

Naylor et al (2017) explored the portrayal of badger vaccination in the national, regional, and farming press, focussing on three primary framings: science versus practicality, badger vaccination versus culling, and victim versus culprit. Media articles often presented conflicting evidence regarding the efficacy of badger vaccination, leading to confusion and a lack of clear policy direction. The debate often juxtaposed scientific findings with practical considerations, such as the feasibility and cost-effectiveness of implementing vaccination programmes. Vaccination was generally portrayed as more humane, but less likely to be immediately effective compared to culling; farming press showed more support for culling, while the national and regional press were more divided, reflecting broader public perspectives. Government was frequently criticized for its handling of bTB control policies. The inconsistent portrayal of scientific evidence and the fluctuating political agenda further complicate public understanding and policymaking.

Enticott et al (2020) found that implementation of biosecurity measures was low, with badger-proofing feed stores the most common; farmers in vaccination areas were more likely to adopt new biosecurity measures, such as fencing off badger latrines and setts. A lack of trust in the government's ability to manage bTB effectively contributed to negative farmer attitudes towards vaccination. The study found evidence of risk compensation behaviours, with farmers in the vaccination area showing increased cattle movements despite the vaccination intervention, influenced by their low self-efficacy and fatalistic attitudes towards disease prevention. Additional measures are needed to support farmers to adopt more comprehensive biosecurity; effective communication and trust-building between farmers and government agencies are crucial to the success of vaccination programmes and broader disease management strategies.

Maye et al (2020) evaluated the Badger Vaccine Deployment Project (BVDP) in England. High bTB prevalence in the BVDP area influenced farmer perceptions and acceptance of badger vaccination. Direct observation of badger vaccination and involvement in the process increased farmer confidence in the vaccination programme. Overall, trust in government bTB policy remained low, but farmers involved in the BVDP reported slightly higher trust levels compared to those in non-vaccination areas.

Conclusion

The natural science evidence base is consistent with BCG vaccination reducing the susceptibility of badgers to *M. bovis* infection. Various large- and small-scale BCG vaccination studies have been, and continue to be, undertaken in the UK and Ireland. There is a stated desire in the UK and Ireland to pivot from badger culling to badger vaccination, should disease surveillance support such a move. Many of these studies report on vaccination logistics, rather than the field efficacy of BCG vaccination in badgers, and more importantly, the effect of badger BCG vaccination on bTB levels in cattle.

Although highly context-dependent (i.e. much of the landscape had already been subjected to reactive badger culling for several years), the most relevant field trial-based evidence derives from the well-controlled and powered “non-inferiority” trial undertaken in Ireland, which showed that badger BCG vaccination, in context, as carried out in the trial, was not inferior to (i.e. no worse than) targeted badger culling in most, but not all, trial areas. This informed a move to replace reactive badger culling with badger BCG vaccination in a >20,000km^2 area in Ireland.

However, effective vaccination depends on vaccine efficacy and vaccination coverage logistics; both important metrics are currently being estimated for Ireland. Whether badger BCG vaccination, alongside all current and potentially future cattle and wildlife control measures, will be sufficient to control and eradicate bTB in Ireland is the subject of ongoing research.

Whether these findings are currently generalisable to the different context in Northern Ireland is worth considering. For example, Ireland has transitioned from decades of reactive badger culling towards badger BCG vaccination; Northern Ireland has a denser badger population and badger culling has not been policy. Advanced mathematical modelling, with parameters derived from the Northern Ireland context, may be informative.

Modelling

In total, ten articles that used mathematical modelling to describe the epidemiology, surveillance, and control of bovine tuberculosis (bTB) are summarized below. Of these, three were review articles (Hayes et al 2023, Smith et al 2018, White et al 2018). Two of the three reviews covered multiple diseases in multiple wildlife species in a variety of different geographical contexts so were of less value to this summary (Hayes et al 2023, White et al 2018).

Bovine tuberculosis prevalence in badgers and cattle

Without any control or intervention applied to the badger population, bTB prevalence in the badger population stabilized at 14% (Smith and Budgey 2021), 15% in Northern Ireland (Courcier et al 2018) and 18% in England (Smith et al 2016). Adbou et al (2016) distinguished between the prevalence of badgers with latent/exposed bTB infections (13.6%) and infectious badgers (45.2%).

Without any badger interventions, bTB cattle herd breakdowns stabilized at 6.5% and 7.3% for simulations based on parameters from a high incidence area of England and Northern Ireland respectively (Smith et al 2016).

Impact of interventions on the badger population

The most effective method for controlling bTB in the badger population, in terms of both bTB prevalence in badgers and number of infectious badgers, was proactive culling with 100% geographical coverage (Abdou et al 2016). However, this led to extinction within 10-12 years from the onset of proactive culling in 14% of simulations and, in the remainder of simulations, the badger population took 25 years to recover (Abdou et al 2016). After 4 years of intensive culling in a high bTB herd incidence area, Smith et al (2021) found that the badger population reduced by a third but then the badger population recovered in about 10 years if culling stopped.

The next best control method was 5 years of proactive culling following by 15 years of trapping, testing and, based on test results, either culling or vaccinating with 100% geographical coverage (Abdou et al 2016). This produced a 98.6% reduction in bTB prevalence in badgers and a 98.5% reduction in infectious badgers (Abdou et al 2016). Similar results were obtained by 5 years of proactive culling followed by oral vaccination with 100% geographical coverage. This modelled scenario produced a 92.0% reduction in bTB prevalence in badgers and a 91.5% reduction in infectious badgers (Abdou et al 2016).

After an initial 4-year intensive badger cull in a high incidence area, ongoing intermittent culling, vaccination alone, or vaccination with fertility control, all had a similar predicted impact on the number of infected badgers (Smith and Budgey, 2021).

Proactive culling, vaccination and trapping, testing and, based on test result, either culling or vaccinating (TVR), all reduced the number of infected badgers in the intervention area (Smith et al 2016). Once the surrounding areas were considered, if TVR did not cause any perturbation in the badger population, this gave the greatest reduction in the number of infected badgers. However, if TVR resulted in perturbation in the badger population, it had no beneficial effect and proactive culling and vaccination had a similar reduction on the number of infected badgers (Smith et al 2016). Selective culling (TVR) did result in an 83% reduction in the number of badgers killed (Smith et al 2016).

In contrast, Bolzoni et al (2020) concluded that localized culling of wildlife may represent an ineffective strategy in limiting infectious disease transmission because localized culling in one patch increased the number of infected wildlife in the other patch. This was always true with reactive culling but only with proactive culling when the intensity of culling was low or when wildlife density was low allowing high dispersal rate.

Impact of interventions on the bovine population

Infection in one species is critically dependent on amplification and feedback from the other host species making control difficult and the impact of control measures highly variable (Brooks-Pollock et al 2015).

Proactive culling, vaccination and TVR, all reduced the number of cattle herd breakdowns in the intervention area (Smith et al 2016). Once the surrounding areas were considered, if TVR did not cause any perturbation in the badger population, this gave the greatest reduction in the number of cattle herd breakdowns. However, if TVR results in perturbation in the badger population, the impact on cattle herd breakdowns were similar for proactive culling and vaccination with neither having a clear beneficial effect (Smith et al 2016).

The Birch et al (2018) model supported the hypothesis that there is a relatively static environmental reservoir of infection on and around some herds that are important in maintaining infection in high incidence regions. However, only a minority of herds in high bTB incidence regions are exposed to environmental sources of infection and not all exposed herds become infected. Therefore, the study concluded that measures aimed at reducing transmission from the environment to cattle may require substantial input to achieve an impact i.e. a high proportion of wildlife may need culling or vaccinating for benefit to the cattle population to be perceived which have implications for cost effectiveness (Birch et al 2018).

Brooks-Pollock et al (2015) demonstrated that cattle bTB prevalence is only sensitive to interventions in the badger population when close to the eradication threshold and the authors hypothesizes that the current bTB epidemic is not close to eradication making control challenging. Therefore, reducing badger-to-cattle transmission is more likely to be effective than reducing prevalence in the badger population, which may have implications for badger vaccination programmes (Brooks-Pollock et al 2015).

Moustakas and Evans (2015) and Smith et al (2018) who concluded that, whilst culling badgers did lower the incidence of bTB in cattle, it was not capable of eradicating the disease. In models that included badger transmission, most of the variance in the prevalence of bTB in cattle was explained by the proportion of cattle being moved, the frequency of bTB testing in cattle and the badger-to-cattle transmission rate (Moustakas and Evans 2015). Birch et al (2018) estimated that cattle-to-cattle transmission was responsible for 64% of infected cattle and environmental reservoirs were the source of infection for 36% of infected cattle and that cattle movements alone were sufficient to generate the observed levels of bTB in low incidence area. All the scenarios that resulted in bTB eradication involved testing cattle at least once a year (Moustakas and Evans 2015). This finding was valid even if the test is imperfect and there was no badger culling. In model without badgers, farm size and winter housing had a significant impact on cattle-to-cattle transmission (Moustakas and Evans 2015).

Using data obtained from the Kilkenny study (ROI), Chang et al (2024) developed a two-host model. The model suggested that cattle-to-cattle transmission contributes most to new cattle infections at the individual cattle level, while breakdowns at the herd level usually involve multiple routes. Badger vaccination, when combined with the cattle test-and-removal programme, may not be sufficient to achieve eradication in this region and there is a need for additional interventions for both species.

Conclusion

It is difficult to generalize model outputs given they are context dependent and indeed all the models are highly abstracted constructs i.e. not field trials. Some modeling outputs suggest that effective proactive culling is best at reducing bTB levels, but this can lead to a prolonged badger population recovery period or even extinction. Using NI data, one model suggested that TVR would deliver the biggest reduction in cattle bTB level provided there was no increased badger perturbation. If badger perturbation occurred, all intervention outputs were similar (proactive culling, TVR, vaccination). Other models highlight the heterogeneity of cattle and badger infections within an area, which adds to the complexity of making generalized statements. Another model suggested that badger intervention was only fully effective at reducing cattle bTB levels when the areas were close to their eradication threshold. Importantly, modelling indicated that the variation in cattle bTB levels was related to cattle movements, bTB testing frequency and interspecies transmission rates, which may reflect the differences seen between different bTB hotspots (see Transmission dynamics section).

Socio-economics

It is increasingly recognised that the answers to disease control lies beyond understanding the science and requires the ability to translate science into behavioural change. This is especially true for a disease such as bTB, which is described as a “wicked problem” due to conflicting values that are difficult to define and resist resolution, governance structures that cross multiple jurisdictions and levels of authority and wide-ranging economic implications that affect a wide range of stakeholders (Fournier et al 2015). Nine social science papers have been summarised. Of these, 3 were reviews and 6 were primary research. A thematic review of 141 social science papers found that 69% were economic analysis and 69% were about social and culture aspect of bTB control (Fournier et al 2015).

Economics

Caminiti et al (2016) reviewed 8 papers regarding the economic evidence for the control or eradication of bTB. Assigning values to all costs and benefits associated with an intervention can be complex and, as a result, many studies were not conclusive. In this review, three studies concluded that the control or eradication of bTB is cost effective, three concluded that it was not and two did not address the question of whether it was cost effective. However, one of the articles that did not find bTB control cost effective excluded the impact of bTB on humans and the authors commented that, “if human health had been considered, bTB control would be beneficial”. In addition, another one of the articles that did not find bTB control cost effective only considered wildlife interventions. Overall, the authors of the review felt that “efforts to control or eradicate bTB may be effective in reducing disease prevalence, economically viable and worth doing.” However, the independent expert panel that devised the UK badger cull study concluded that proactive culling was not cost-effective and caused a reduction in biodiversity (Lederman 2016). Based on the data provided for England, badger culls in the UK therefore may be unjustified (Lederman et al 2021).

Several articles addressed the issue of cost sharing. According to Maye et al (2017), when farmers were given a choice about which control strategy to employ but were told they would have to pay for their chosen strategy, farmers felt this was the ‘ideal approach’ and had no concerns about the financial implications. Farmers in an annual testing area of England and Wales were willing to pay between £17 – 55 per animal for a cattle vaccine if it had a 90% efficacy at reducing the risk of a herd breakdown and they were insured for 100% of losses (Bennett 2017). In contrast, in Northern Ireland, there was a high level of disagreement between farmers on their willingness to pay for bTB control measures (O’Hagan et al 2016). For example, 53% would support pre-movement testing of cattle but only 17% would be willing to pay for it, 80% would allow badger culling on their land but only 20% would be willing to pay for it, 82% would support badger vaccination but only 19% would be open to paying for it. The farmers’ age was associated with their willingness to pay for bTB control measures (O’Hagan et al 2016).

Social and Cultural

Public perception in relation to badger culling policies can be evaluated by monitoring social media, both prior to, and after implementation. This can identify and address areas of miscommunication and misinformation to improve public support for policies. (Dicks et al 2021). A recent study into the media coverage of badger culling revealed that both the BBC and commercial rivals reported on competing voices and perspectives in a balanced way. It was found that the issue was framed as a conflict over badgers rather than about the spread of a disease affecting livestock and livelihoods, and there was focus on a narrow set of voices involved in the conflict (Stanyer 2021).

When discussing issues such as badger culling policies, it may be beneficial to move beyond particular entrenched adversarial patterns and to discuss areas of the debate less likely to encourage participants to talk past one another (Keenan et al 2020). When discussions take place, it is important to be both an ‘insider’ and ‘outsider’ with all participant groups to maintain a degree of access across multiple sides of a controversy (Phoenix 2024). Diplomacy in relation to resolving conflicting views on badger culling can be started by acknowledging the different positions (‘ethical empiricist’ (evidence is based on experience), ‘nostalgic autonomist’ (independent thinking) and ‘liberal pragmatist’ (thoughts focusing on supporting individual rights)) (Price et al 2017).

Maye et al (2017) constructed four potential bTB control scenarios and interviewed 50 farms in England to determine what action they would take and where they would seek advice. Most farmers had a positive perception of badger culling but there was a fear of public perception and sabotage. Their decisions regarding badger culling were most likely to be influenced by peer-pressure, their private vet and farming organisations. In contrast, government organisations were not influential. For strategies involving vaccination, whether badgers or cattle, government organisation were more influential. Broughan et al (2016b) found that farms with bTB (OTF-W farms) in emerging endemic areas of GB were less likely to be influence by government vets or other farmers than farms without bTB (OTF farms). A GB survey of over 300 farmers (117 with bTB and 220 without bTB) indicated that farmers believed they were unable to do anything about bTB but were keen for the government intervention to help control the spread of bTB (Enticott 2015). In a convenience sample study relating to bTB biosecurity, 'most farmers interviewed felt utterly powerless and in an 'intractable' position which prompted a sense of despair that 'paralysed' them and made new learning unappealing and, seemingly, pointless' (Hamilton et al 2019).

Using RBCT data, cattle movement practices were compared across proactive, reactive and control areas (Brunton and Enticott 2024). It was found that proactive badger culling was not associated with risk compensation behaviours, while reactive badger culling was associated with decreased risk taking among farmers.

In Wales, there were moderate levels of general public support for badger culling, but in general it was not believed that the current scientific evidence on the effectiveness of a cull is acceptable. People from rural fringe areas and areas with low disease incidence were more likely to favour badger vaccination over culling (Enticott 2015).

Less than half of GB farmers (39%) believed that improving biosecurity can reduce the risk of a bTB breakdown and most (71%) believed they cannot prevent a bTB breakdown (Bennett 2017). However, OTF-W herds in emerging endemic area were more likely to have implemented biosecurity measures relating to badger control but biosecurity regarding cattle controls were similar to OTF herds (Broughan et al 2016b). According to Maye et al (2017), farmers were more receptive to cattle vaccination than badger vaccination as a control strategy, although they had concerns about the cost of cattle vaccination. O'Hagan et al (2016) found that most farmers surveyed in Northern Ireland preferred badger vaccination to culling (55% versus 26%).

There is considerable variation in the societal attitudes to the management of wildlife across Europe relating to the apparent conflict between conservation, animal welfare, and management goals, as well as cultural differences in the acceptability of pursuits such as hunting (Allen et al 2018). Badger interventions in particular are challenging due to competing and conflicting stakeholder opinions. Gormley et al (2018) summarised attitudes to wildlife reservoirs for bTB and wildlife control in seven countries. They concluded that attitude to wildlife management will depend on the status of the animal i.e. is it considered a pest or a conservation priority, the value that society assigned to the species, the type of intervention proposed, ethical issues associated with wildlife management and the economic cost-benefit of wildlife management. In addition, the value assigned to a species was influenced by their economic importance, nutritional value, ecological role and socio-cultural significance. Therefore, when the value placed on a particular species is high, wildlife interventions demand exceptionally high-quality scientific evidence. Gormley et al (2018) commented that, in Northern Ireland, "a one size fits all approach" is unlikely to succeed. Bennett (2017) did a case study in GB, regarding the general publics' attitude to badgers and badger control. Whilst the general public felt that controlling bTB was important, respondents were willing to pay £63 per household not to cull badgers but only £1.52 per household per 10,000 fewer cattle slaughtered. Most of the general public felt that controlling the badger population was acceptable if it did not involve killing badgers and felt that the government should be responsible for badger control. However, just over half would accept a limited and temporary cull of badgers if it helped control bTB (Bennett 2017).

An online survey of 300 farmers in the Burren, County Clare, frequently mentioned wildlife, both badgers and goats, during their interview regarding bovine TB (Clarke et al 2022). Many felt that more needed to be done about badgers and further research was required into the risk posed by feral goats; although research had so far not found bTB present in the feral goat population (Clarke et al 2022).

Conclusion

Fournier et al (2015) highlighted three potential “promising approaches”: enhanced participation, collaboration and engagement of stakeholder in decision making, proactive incorporation of scientific evidence and the importance of contextualising as the local context will influence stakeholder acceptance and compliance. Robinson (2019) considered it important to focus on the pathogen, select language carefully when discussing bTB and invest in new innovations, such as vaccines and diagnostic tests.

Miscellaneous

This section includes articles relating to bTB research conducted in France with specific reference to badgers and also one paper that discusses badger population control using contraceptive injection.

French studies

There have been increased bTB herd infection levels in certain areas of France in recent years. Bouchez-Zacria et al (2018) observed that the French situation was multifactorial with *M. bovis* transmission between cattle farms differing across areas, which was driven by variations in cattle trade, pasture management and badger networks (based on *M. bovis* molecular type information). A national *M. bovis* wildlife surveillance system in France (Sylvatub), which used targeted surveillance of badgers, wild boar and deer, found 4-5% of badgers infected and 2-3% of wild boar infected (Réveillaud et al 2018). The same *M. bovis* genotype was found in the local wildlife and cattle.

A further study showed that infected badgers were trapped closer to infected farms (Bouchez-Zacria et al 2023a). However, when low resolution strain typing information (spoligotype) was taken into account, no association was found between cattle and badger strain types. Further work on spatial associations (Bouchez-Zacria et al 2024) found that the probability for a sett to be infected was associated with the proportion of neighbouring setts that were infected (OR: 3.19 [95% CI 2.04 – 5.17]) and the presence of nearby pastures belonging to an infected farm (OR: 2.33 [95% CI 1.13 – 4.89]). While badger culling measures have been implemented in France in the vicinity of infected farms and their pastures since 2012, this study highlighted the need to reinforce measures aimed at reducing both within-species and between-species infection pressure by considering use of badger vaccination along with biosecurity measures.

Modelling of bTB related data (2007-2011) from south-west France (Bouchez-Zacria et al 2023b) estimated that the effective reproduction number (R) was estimated to be 1.34. This indicated a self-sustaining *M. bovis* transmission by a maintenance community although within-species Rs were both < 1, signifying that neither cattle nor badger populations acted as separate reservoir hosts. From 2012, control measures were implemented, and Rs decreased below 1. The spread of *M. bovis* was more rapid from cattle farms (generation time = 0.5–0.7 year) than from badger groups (generation time =1.3–2.4 years). Although eradication of bTB appears possible in this study area (since R < 1), the model suggested it was a long-term prospect, because of the prolonged persistence of infection in badger groups (2.9–5.7 years).

A TVR approach is being currently trialled in France (Boschiroli 2023).

Fertility control

One study looked at the feasibility of controlling badger populations using immunological contraception (Cowan et al 2019). Badgers were vaccinated with a single-shot injectable immune-contraceptive vaccine (*Gonacon*) targeting gonadotropin-releasing hormone (GnRH). The optimal badger vaccination window was considered narrow (June – August). Vaccination would need to be repeated at least every 2 years in order to maintain levels of female infertility predicted to have demographic impacts on badger populations. No negative welfare consequences were observed in vaccinated badgers. However, as with other interventions, trapped badgers would have a negative impact evaluation on badger welfare (Collof et al 2024).

A simulation model of the impact of post-badger cull strategies in England indicated that there was little difference in outputs between various intermittent culling regimes, badger vaccination and use of a vaccine combined with fertility control (Smith and Budgey 2021).

Future focus

A review of bTB epidemiology and control in the UK and ROI concluded that 30 years of research have demonstrated that badgers contribute to the epidemiology of bTB in cattle (Ni Bhuachalla et al 2015). As a result, it is unlikely that bTB will be eradicated in the cattle population without the reservoir of *M. bovis* in the badger population being controlled. When considering different control strategies to reduce badger-to-cattle transmission, they noted that there were no field trials demonstrating a sustained reduction in cattle bTB incidence because of biosecurity measures alone. Due to the lack of public support for large scale culling, they suggested that vaccination was likely to be the most acceptable option but that the approach to vaccination in badgers will need to be adapted to the badger population (Ni Bhuachalla et al 2015). Whilst McCulloch et al (2017e) agreed that badger vaccination was the ideal control method in the badger population, their reasoning was based on a utilitarian argument. The authors concluded that “bTB badger control should not, and indeed cannot, be made simply based on the scientific evidence base, or by use of economic cost-benefit analysis. Ultimately, policy on badger control is necessarily a moral issue and should be addressed in the context of the following question: ethically, what is the *right*, or most justifiable, policy on badger control considering impacts on all morally relevant affected groups?” and, as a result, “non-culling approaches, particularly badger vaccination, result in greater total utility, compared to badger culling.”

In a review of the direction of future bTB policy in England, widespread badger culling was to be replaced with badger vaccination and targeted badger culling in specific circumstance (McCormack et al 2023). However, this was alongside other innovations including:

1. **knowledge-based trading** based on a farm’s last bTB breakdown and the length of the previous bTB breakdown which generates a health score that is publicly available.
2. **whole genome sequencing**, which is already done at herd level, but will expand to include phylogenetic analysis and GIS data,
3. development of a **cattle vaccination with a DIVA test**. Phase 1 began in 2021 but both the vaccine and the DIVA test will require World Organisation for Animal Health (WOAH) approval to maintain international trade.
4. the development, evaluation and use of **molecularly defined tuberculin** (MDT) to create a more standardised reagent, which will reduce batch variation and improve consistency of bTB testing.

Similarly, Robinson (2019) emphasised the importance of laboratories for the advancement of diagnostic techniques, vaccines and epidemiology, including whole-genome sequencing.

With the ROI situation, a review highlighted bTB persistence in a herd or area as a key feature of the infection with much variability in the bTB risk across the national herd (More and Good 2015). They highlighted three main drivers for policy change (scientific advances, improvements in programme support and ongoing programme review). A key concern is the amount of additional effort that will be required to move towards final eradication along with the need to re-engage with the farming community who should play a much greater role in ownership (responsibility and cost sharing) of the bTB programme. In a later article, More (2019) suggested that all current strategies plus badger vaccination would not be sufficient to successfully eradicate bTB from Ireland by 2030. He proposed that additional measures were required relating to adequately addressing bTB risks from wildlife, implementing additional risk-based cattle controls, and enhancing industry engagement. A more recent publication based on Spanish findings also concluded the need to target both cattle management and wildlife factors for successful bTB control in grazing-based farming systems (Herrero-García et al 2024).

Concluding remarks

Peer reviewed published research between 2015 and May 2024 has provided supplemental evidence on the various aspects of badger intervention. On the practical level, all previously identified badger intervention methods (proactive culling, selective culling and vaccination) have been trialled. Of particular note, is the switch from culling to vaccination in ROI (although limited culling is retained as an option in hotspot areas) and the proven utility of real time trap side testing of badgers for *M. bovis* infection. Selective culling combined with vaccination was only completed within one area (NI TVR study) hence limiting extrapolation of its results (although a similar approach is currently being piloted in France).

While there continues to be disparity of analytical/statistical opinion on the outputs relating to the RBCT, new evidence suggests that the Badger Control Policy (BCP) implemented in areas of England appears to have been effective in decreasing cattle bTB levels. However, the BCP included aspects over and above direct badger intervention and additional bTB cattle control measures have also been contemporaneously introduced within the high risk area of England. Indeed, for any badger intervention to succeed in the longer term, bTB control measures in cattle also need to be effective in reducing or preventing bTB re-introduction to the area as well as limiting re-infections of the badger population (through badger movement or cattle-badger transmission).

With respect to badger vaccination, injectable vaccine is still the only viable option as there are logistical obstacles relating to oral bait vaccine delivery. This means that badgers do need to be captured to enable vaccination or testing, which does pose a welfare issue. However, actual physical injuries seem to be minor in most of badgers captured by cages or stopped restraints.

Modelling outputs do tend to demonstrate that badger intervention can reduce bTB levels with methods involving a lethal component (proactive or selective culling) providing a faster bTB response than vaccination only. However, there has been an increase in publications on the socio-economic aspects of bTB in relation to stakeholder knowledge, opinions and behaviours related to badger intervention options. They tend to highlight the need to consider ethics and public opinion as well as any scientific evidence base in relation to badger intervention.

Importantly, effective, positive engagement by all stakeholders is required to enable bTB eradication.

References

Abdou, M., K. Frankena, J. O'Keeffe, Byrne, A.W. (2016). Effect of culling and vaccination on bovine tuberculosis infection in a European badger (*Meles meles*) population by spatial simulation modelling. *Preventive Veterinary Medicine* 125: 19-30. DOI: 10.1016/j.prevetmed.2015.12.012.

Akhmetova, A., Guerrero, J., McAdam, P., Salvador, L.C.M,. Crispell, J., Lavery, J., Presho, E., Kao, R.R., Biek, R., Menzies, F., Trimble, N., Harwood, R., Pepler, P.T., Oravcova, K., Graham, J., Skuce, R., du Plessis, L., Thompson, S., Wright, L., Byrne, A.W., Allen, A.R. (2023). Genomic epidemiology of *Mycobacterium bovis* infection in sympatric badger and cattle populations in Northern Ireland. *Microbial Genomics* 9:1023. doi: 10.1099/mgen.0.001023

Allen, A. R., Skuce, R.A., Byrne, A.W. (2018). Bovine Tuberculosis in Britain and Ireland - A Perfect Storm? the Confluence of Potential Ecological and Epidemiological Impediments to Controlling a Chronic Infectious Disease. Frontiers in Veterinary Science 5. DOI: 10.3389/fvets.2018.00109.

Allen, A., Milne, G., McCormick, C., Collins, S., O'Hagan, M., Skuce, R., Trimble, N., Harwood, R., Menzies, F., Byrne, A.W. (2022). European badger (*Meles meles*) responses to low-intensity, selective culling: Using mark–recapture and relatedness data to assess social perturbation. *Ecological Solutions and Evidence* 3(3). DOI: 10.1002/2688-8319.12165.

Arnold, M. E., Courcier, E. A., Stringer, L.A., McCormick, C.M., Pascual-Linaza, A.V., Collins, S.F., Trimble, N.A., Ford, T., Thompson, S., Corbett, D., Menzies, F.D. (2021). A Bayesian analysis of a test and vaccinate or remove study to control bovine tuberculosis in badgers (*Meles meles*). *PLoS ONE* 16(1 January). DOI: 10.1371/journal.pone.0246141.

Ashford, R. T., Anderson, P., Waring, L., Davé, D., Smith, F., Delahay, R.J., Gormley, E., Chambers, M.A., Sawyer, J., Lesellier, S. (2020). Evaluation of the Dual Path Platform (DPP) VetTB assay for the detection of *Mycobacterium bovis* infection in badgers. *Preventive Veterinary Medicine* 180. DOI: 10.1016/j.prevetmed.2020.105005.

Aznar, I., Frankena, K., More, S.J., O'Keeffe, J., McGrath, G., de Jong, M.C.M. (2018). Quantification of *Mycobacterium bovis* transmission in a badger vaccine field trial. *Preventive Veterinary Medicine* 149: 29-37. DOI: 10.1016/j.prevetmed.2017.10.010.

Bacigalupo, S. A., Dixon, L.K., Gubbins, S., Kucharski, A.J., Drewe, J.A. (2020). Towards a unified generic framework to define and observe contacts between livestock and wildlife: A systematic review. *PeerJ* 8. DOI: 10.7717/peerj.10221.

Balseiro, A., Thomas, J., Gortázar, C., Risalde, M.A. (2020a). Development and Challenges in Animal Tuberculosis Vaccination. *Pathogens* 9(6). DOI: 10.3390/pathogens9060472.

Balseiro, A., Prieto, J.M., Álvarez, V., Lesellier, S., Davé, D., Salguero, F,J, Sevilla, I.A., Infantes-Lorenzo, J.A., Garrido, J.M., Adriaensen, H., Juste, R.A., Barral, M. (2020b). Protective Effect of Oral BCG and Inactivated *Mycobacterium bovis* Vaccines in European Badgers (*Meles meles*) Experimentally Infected With *M. bovis*. *Frontiers in Veterinary Science* 7. DOI: 10.3389/fvets.2020.00041.

Barroso, P., Breslin, P., McGrath, G., Madden, J.M., Tratalos, J.A., More, S.J., Ryan, E., Byrne, A.W., Barrett, D. (2022). Is there an association between road building and bovine tuberculosis herd risk? A three time-point study in Ireland, 2011-2019. *Preventive Veterinary Medicine* 198. DOI: 10.1016/j.prevetmed.2021.105542.

Bennett, R.M. (2017). The political economy of bovine tuberculosis in Great Britain. OIE Revue Scientifique et Technique 36(1): 105-114. DOI: 10.20506/rst.36.1.2614.

Benton, C.H., Delahay, R.J., Robertson, A., McDonald, R., Wilson, A.J., Burke, T.A., Hodgson, D. (2016). Blood thicker than water: Kinship, disease prevalence and group size drive divergent patterns of infection risk in a social mammal. Proceedings of the Royal Society B: Biological Sciences 283(1835). DOI: 10.1098/rspb.2016.0798.

Benton, C.H., Phoenix, J., Smith, F.A.P., Robertson, A., McDonald, R.A., Wilson, G., Delahay, R.J. (2020). Badger vaccination in England: Progress, operational effectiveness and participant motivations. People and Nature 2(3): 761-775. DOI: 10.1002/pan3.10095.

Benton, C.H., Phoenix, J., Robertson, A., Delahay, R.J. (2023). Vaccinating badgers in a post-cull landscape; insights from the field. Ecological Solutions and Evidence 4(1). DOI: 10.1002/2688-8319.12208.

Benton, C.H., Griffiths, A.L., Delahay, R.J. (2024). Performance of fur clips and livestock markers for identifying vaccinated badgers. *European Journal of Wildlife Research* 70(2). DOI: 10.1007/s10344-024-01789-0.

Bianco, C., Lesellier, S., Barrat, J., Richomme, C., Boschiroli, M.L., Núñez, A. (2020). Subclinical BCG-osis in a Captive Badger (*Meles meles*) with Lymphoma. *Journal of Comparative Pathology* 176: 76-80. DOI: 10.1016/j.jcpa.2020.02.009.

Bielby, J., Vial, F., Woodroffe, R., Donnelly, C.A. (2016). Localised badger culling increases risk of herd breakdown on nearby, not focal, land. *PLoS ONE* 11(10). DOI: 10.1371/journal.pone.0164618.

Bilham, K., Boyd, A.C., Preston, S.G., Buesching, C.D, Newman, C., Macdonald, D.W., Smith, A.W. (2017). Badger macrophages fail to produce nitric oxide, a key anti-mycobacterial effector molecule. *Scientific Reports* 7. DOI: 10.1038/srep45470.

Birch, C.P.D., Goddard, A., Tearne, O. (2018). A new bovine tuberculosis model for England and Wales (BoTMEW) to simulate epidemiology, surveillance and control. BMC Veterinary Research 14(1). DOI: 10.1186/s12917-018-1595-9.

Birch, C.P.D., Chambers, M.A., Lesellier, S. (2021). A combined measure of tuberculous lesions for assessing the efficacy of vaccination against tuberculosis (Mycobacterium bovis) in European badgers (Meles meles) supports the 3Rs principle of reduction. Vaccine 39(11): 1661-1666. DOI: 10.1016/j.vaccine.2019.10.079.

Birch, C.P.D., Bakrania, M., Prosser, A., Brown, D., Withenshaw, S.M., Downs, S.H. (2024). Difference in differences analysis evaluates the effects of the badger control policy on bovine tuberculosis in England. *Scientific Reports* 14(1). DOI: 10.1038/s41598-024-54062-4.

Boggiatto, P.M., Kanipe, C.R., Putz, E.J., Olsen, S.C., Palmer, M.V. (2023). Wildlife Immune Responses to *Mycobacterium bovis* and to Bacille of Calmette-Guerin. *Journal of immunology* 211(8): 1173-1179. DOI: 10.4049/jimmunol.2300323.

Bolzoni, L., Della Marca, R., Groppi, M., Gragnani, A. (2020). Dynamics of a metapopulation epidemic model with localized culling. *Discrete and Continuous Dynamical Systems-Series B* 25(6): 2307-2330. DOI: 10.3934/dcdsb.2020036.

Boschiroli, M.L. (2023). Animal tuberculosis control in a disease-free country, France: does the long and winding road really lead to eradication? *Irish Veterinary Journal* 76(Suppl 1): 25. DOI: 10.1186/s13620-023-00258-5.

Bouchez-Zacria, M., Courcoul, A., Durand, B. (2018). The Distribution of Bovine Tuberculosis in Cattle Farms Is Linked to Cattle Trade and Badger-Mediated Contact Networks in South-Western France, 2007–2015. *Frontiers in Veterinary Science* 5. DOI: 10.3389/fvets.2018.00173.

Bouchez-Zacria, M., Payne, A., Girard, S., Richomme, C., Boschiroli, M.L., Marsot, M., Durand, B., Desvaux, S. (2023a). Spatial association of *Mycobacterium bovis* infection in cattle and badgers at the pasture interface in an endemic area in France. *Preventive Veterinary Medicine* 220. DOI: 10.1016/j.prevetmed.2023.106044.

Bouchez-Zacria, M., Ruette, S., Richomme, C., Lesellier, S., Payne, A., Boschiroli, M.L., Courcoul, A., Durand, B. (2023b). Analysis of a multi-type resurgence of *Mycobacterium bovis* in cattle and badgers in Southwest France, 2007-2019. *Veterinary Research* 54(1): 41. DOI: 10.1186/s13567-023-01168-8.

Bouchez-Zacria, M., Jabert, P., Réveillaud, É., Richomme, C., Marsot, M. (2024). Intra- and interspecies infectious neighbourhoods as determinant parameters for *Mycobacterium bovis* infection among badgers in southwestern France. *Preventive Veterinary Medicine* 225. DOI: 10.1016/j.prevetmed.2024.106146.

Brooks-Pollock, E., Wood, and J.L.N. (2015). Eliminating bovine tuberculosis in cattle and badgers: Insight from a dynamic model. *Proceedings of the Royal Society B: Biological Sciences* 282(1808). DOI: 10.1098/rspb.2015.0374.

Broughan, J.M., Judge, J., Ely, E., Delahay, R.J., Wilson, G., Clifton-Hadley, R.S., Goodchild, A.V., Bishop, H., Parry, J.E., Downs, S.H. (2016a). A review of risk factors for bovine tuberculosis infection in cattle in the UK and Ireland. *Epidemiology and Infection* 144(14): 2899-2926. DOI: 10.1017/s095026881600131x.

Broughan, J.M., Maye, D., Carmody, P., Brunton, L. A., Ashton, A., Wint, W., Alexander, N., Naylor, R., Ward, K., Goodchild, A.V., Hinchliffe, S., Eglin, R.D., Upton, P., Nicholson, R., Enticott, G. (2016b). Farm characteristics and farmer perceptions associated with bovine tuberculosis incidents in areas of emerging endemic spread. *Preventive Veterinary Medicine* 129: 88-98. DOI: 10.1016/j.prevetmed.2016.05.007.

Brunton, L.A., Donnelly, C.A., O'Connor, H., Prosser, A., Ashfield, S., Ashton, A., Upton, P., Mitchell, A., Goodchild, A.V., Parry, J.E., Downs, S.H. (2017). Assessing the effects of the first 2 years of industry-led badger culling in England on the incidence of bovine tuberculosis in cattle in 2013–2015. *Ecology and Evolution* 7(18): 7213-7230. DOI: 10.1002/ece3.3254.

Brunton, L., Enticott, G. (2024). Is badger culling associated with risk compensation behaviour among cattle farmers? *Veterinary Record* 194(11): e4152. DOI: 10.1002/vetr.4152. Open Access

Buddle, B.M., Vordermeier, H.M., Chambers, M.A., de Klerk-Lorist, L.M. (2018). Efficacy and Safety of BCG Vaccine for Control of Tuberculosis in Domestic Livestock and Wildlife. *Frontiers in veterinary science* 5: 259. DOI: 10.3389/fvets.2018.00259.

Buzdugan, S.N., Chambers, M.A., Delahay, R.J., Drewe, J.A. (2016). Diagnosis of tuberculosis in groups of badgers: an exploration of the impact of trapping efficiency, infection prevalence and the use of multiple tests. *Epidemiology and Infection* 144(8): 1717-1727. DOI: 10.1017/S0950268815003210.

Buzdugan, S.N., Chambers, M.A., Delahay, R.J., Drewe, J.A. (2017a). Quantitative interferon-gamma responses predict future disease progression in badgers naturally infected with *Mycobacterium bovis*. *Epidemiology and Infection* 145(15): 3204-3213. DOI: 10.1017/S0950268817001960.

Buzdugan, S. N., Vergne, T., Grosbois, V., Delahay, R.J., Drewe, J.A. (2017b). Inference of the infection status of individuals using longitudinal testing data from cryptic populations: Towards a probabilistic approach to diagnosis. *Scientific Reports* 7(1). DOI: 10.1038/s41598-017-00806-4.

Byrne, A. W., Kenny, K., Fogarty, U., O'Keeffe, J.J., More, S.J., McGrath, G., Teeling, M., Martin, S.W., Dohoo, I.R. (2015a). Spatial and temporal analyses of metrics of tuberculosis infection in badgers (*Meles meles*) from the Republic of Ireland: Trends in apparent prevalence. *Preventive Veterinary Medicine* 122(3): 345-354. DOI: 10.1016/j.prevetmed.2015.10.013.

Byrne, A.W., O'Keeffe, J., Fogarty, U., Rooney, P., Martin, S.W. (2015b). Monitoring trap-related injury status during large-scale wildlife management programmes: an adaptive management approach. *European Journal of Wildlife Research* 61(3): 445-455. DOI: 10.1007/s10344-015-0916-6.

Byrne, A.W., Do Lin San, E. (2016). A cautionary note on the use of minimum number alive-derived trap ability metrics in wildlife programmes, as exemplified by the case of the European badger (*Meles meles*)," *Wildlife Biology in Practice*, vol. 12, no. 3, 2016.

Byrne, A.W., O'Keeffe, J., Bueesching, C.D., Newman, C. (2019). Push and pull factors driving movement in a social mammal: context dependent behavioral plasticity at the landscape scale. *Current Zoology* 65 (5), 517– 525.

Byrne, A. W., Parnell, A., O'Keeffe, J., Madden, J.M. (2021). The challenge of estimating wildlife populations at scale: the case of the European badger (*Meles meles*) in Ireland. *European Journal of Wildlife Research* 67(5). DOI: 10.1007/s10344-021-01528-9.

Byrne, A. W., Barrett, D., Breslin, P., O'Keeffe, J., Murphy, K.J., Conteddu, K., Morera-Pujol, V., Ryan, E., Ciuti, S. (2022a). Disturbance Ecology Meets Bovine Tuberculosis (bTB) Epidemiology: A Before-and-After Study on the Association between Forest Clearfelling and bTB Herd Risk in Cattle Herds. *Pathogens* 11(7). DOI: 10.3390/pathogens11070807.

Byrne, A.W., O'Keeffe, J., Martin, S.W. (2022b). Factors affecting European badger movement lengths and propensity: evidence of density-dependent effects? in Small Carnivores: *Evolution, Ecology, Behaviour, and Conservation*, 2022.

Byrne, A. W., Allen, A., Ciuti, S., Gormley, E., Kelly, D.J., Marks, N.J., Marples, N.M., Menzies, F., Montgomery, I., Newman, C., O'Hagan, M., Reid, N., Scantlebury, D.M., Stuart, P., Tsai, M.S. (2024). Badger Ecology, Bovine Tuberculosis, and Population Management: Lessons from the Island of Ireland. Transboundary and Emerging Diseases 2024. DOI: 10.1155/2024/8875146.

Caminiti, A., Pelone, F., La Torre, G., De Giusti, M., Saulle, R., Mannocci, A., Sala, M. Della Marta, U., Scaramozzino, P. (2016). Control and eradication of tuberculosis in cattle: a systematic review of economic evidence. *Veterinary Record* 179(3): 70-75. DOI: 10.1136/vr.103616.

Campbell, E.L., Byrne, A.W., Menzies, F.D., McBride, K.R., McCormick, C.M., Scantlebury, D.M., Reid, N. (2019). Interspecific visitation of cattle and badgers to fomites: a transmission risk for bovine tuberculosis? *Ecology and Evolution* 9 (15) 8479-8489, 2019.

Campbell, E. L., Menzies, F.D., Byrne, A.W., Porter, S., McCormick, C.M., McBride, K.R., Scantlebury, D.M., Reid, N. (2020). Grazing cattle exposure to neighbouring herds and badgers in relation to bovine tuberculosis risk. *Research in Veterinary Science* 133: 297-303. DOI: 10.1016/j.rvsc.2020.09.032.

Carter S.P., Chambers M.A., Rushton S.P., Shirley M.D.F., Schuchert P., Pietravalle S., Murray A., Rogers F., Gettinby G., Smith G.C., Delahay, R.J., Hewinson, R.G., MacDonald, R.A. (2012). BCG vaccination reduces risk of tuberculosis Infection in vaccinated badgers and unvaccinated badger cubs. *PLoS ONE 7,* e49833. (doi:10.1371/journal.pone.0049833).

Carter, S.P., Robertson, A., Palphramand, K.L., Chambers, M.A., McDonald, R.A., Delahay, R.J. (2018). Bait uptake by wild badgers and its implications for oral vaccination against tuberculosis*. PLoS ONE* 13(11). DOI: 10.1371/journal.pone.0206136.

Cassidy, A. (2015). Big science' in the field: experimenting with badgers and bovine TB, 1995–2015. *History and Philosophy of the Life Sciences* 37(3): 305-325. DOI: 10.1007/s40656-015-0072-z.

Chambers, M.A., Aldwell, F., Williams, G.A., Palmer, S., Gowtage, S., Ashford, R., Dalley, D.J., Davé, D., Weyer, U., Salguero, F.J., Nunez, A., Nadian, A.K., Crawshaw, T., Corner, L.A.L., Lesellier, S. (2017). The effect of oral vaccination with *Mycobacterium bovis* BCG on the development of tuberculosis in captive European badgers (*Meles meles*). *Frontiers in Cellular and Infection Microbiology* 7(JAN). DOI: 10.3389/fcimb.2017.00006.

Chang, Y., Hartemink, N., Byrne, A.W., Gormley, E., McGrath, G., Tratalos, J.A., Breslin, P., More, S.J., de Jong, M.C.M. (2023). Inferring bovine tuberculosis transmission between cattle and badgers via the environment and risk mapping. *Frontiers in Veterinary Science* 10. DOI: 10.3389/fvets.2023.1233173.

Chang, Y., Widgren, S., de Jong, M.C.M., Tratalos, J.A., More, S.J., Hartemink, N. (2024). Evaluating the effectiveness of badger vaccination combined with cattle test-and-removal in managing Bovine Tuberculosis: Insights from a two-host and multi-route transmission model. *Preventive veterinary medicine* 235: 106386. DOI: 10.1016/j.prevetmed.2024.106386.

Clarke, A., Byrne, A.W., Maher, J., Ryan, E., Farrell, F., McSweeney, C., Barrett, D. (2022). Engaging With Farmers to Explore Correlates of Bovine Tuberculosis Risk in an Internationally Important Heritage Landscape: The Burren, in the West of Ireland. *Frontiers in Veterinary Science* 9. DOI: 10.3389/fvets.2022.791661.

Colloff, A., Baker, S.E., Beausoleil, N.J., Sharp, T., Golledge, H., Lane, J., Cox, R., Siwonia, M., Delahay, R. (2024). Use of an expert elicitation methodology to compare welfare impacts of two approaches for blood sampling European badgers (*Meles meles*) in the field. Animal Welfare 33. DOI: 10.1017/awf.2024.16.

Conteddu, K., English, H.M., Byrne, A.W., Amin, B., Griffin, L.L., Kaur, P., Morera-Pujol, V., Murphy, K.J., Salter-Townshend, M., Smith, A.F., Ciuti, S. (2024). A scoping review on bovine tuberculosis highlights the need for novel data streams and analytical approaches to curb zoonotic diseases. Veterinary research 55(1): 64. DOI: 10.1186/s13567-024-01314-w.

Courcier, E.A., Menzies, F.D., Strain, S.A.J., Skuce, R.A., Robinson, P.A., Patterson, I.A.P., McBride, K.R., McCormick, C.M., Walton, E., McDowell, S.W.J., Abernethy D.A. (2018). Monitoring Mycobacterium bovis in Eurasian badgers (*Meles meles*) killed by vehicles in Northern Ireland between 1998 and 2011. *Veterinary Record* 182, 259-265. doi: 10.1136/vr.103934

Courcier, E.A., Pascual-Linaza, A.V., Arnold, M.E., McCormick, C.M., Corbett, D.M., O'Hagan, M.J.H., Collins, S.J., Trimble, N.A., McGeown, C.F., McHugh, G.E., McBride, K.R., McNair, J., Thompson, S., Patterson, I.A.P., Menzies, F.D. (2020). Evaluating the application of the dual path platform VetTB test for badgers (*Meles meles*) in the test and vaccinate or remove (TVR) wildlife research intervention project in Northern Ireland. *Research in Veterinary Science* 130: 170-178. DOI: 10.1016/j.rvsc.2020.03.007.

Courcier, E. A., Collins, S.F., McCormick, C.M., Arnold, M.E., Corbett, D.M., Ford, T., McGeown, C.F., Barry, C., Kirke, R., Menzies, F.D. (2022). The impact of BCG strains and repeat vaccinations on immunodiagnostic tests in Eurasian badgers (*Meles meles*). *Vaccine* 40(34): 4972-4978. DOI: 10.1016/j.vaccine.2022.06.081.

Cowan, D., Smith, G.C., Gomm, M., Brash, M., Bellamy, F., Massei, G., Conwell, R., Vial, F. (2019). Evaluation of a single-shot gonadotropin-releasing hormone (GnRH) immunocontraceptive vaccine in captive badgers. *European Journal of Wildlife Research* 65(4). DOI: 10.1007/s10344-019-1296-0.

Crispell, J., Benton, C. H., Balaz, D., De Maio, N., Ahkmetova, A., Allen, A., Biek, R. Presho, E.L., Dale, J., Hewinson, G., Lycett, S.J. Nunez-Garcia, J., Skuce, R.A., Trewby, H., Wilson, D.J., Zadoks, R.N., Delahay, R.J., Kao, R.R. (2019). Combining genomics and epidemiology to analyse bi-directional transmission of mycobacterium bovis in a multi-host system. *eLife* 8. DOI: 10.7554/eLife.45833.

Crispell, J., Cassidy, S., Kenny, K., McGrath, G., Warde, S., Cameron, H., Rossi, G. Macwhite, T., White, P.C.L., Lycett, S., Kao, R.R., Moriarty, J., Gordon, S.V. (2020). *Mycobacterium bovis* genomics reveals transmission of infection between cattle and deer in Ireland. *Microbial Genomics* 6(8): 1-8. DOI: 10.1099/mgen.0.000388.

Dicks, F., Marks, T., Karafillakis, E., Chambers, M.A. (2021). Vaccination as a control tool in bovine tuberculosis: Social media monitoring to assess public response to government policy development and implementation. *Vaccines* 9(4). DOI: 10.3390/vaccines9040314.

Donnelly, C.A., Bento, A.I., Goodchild, A.V., Downs, S.H. (2015). Exploration of the power of routine surveillance data to assess the impacts of industry-led badger culling on bovine tuberculosis incidence in cattle herds. *Veterinary Record* 177(16): 417. DOI: 10.1136/vr.103201.

Downs, S.H., Prosser, A., Ashton, A., Ashfield, S., Brunton, L.A., Brouwer, A., Upton, P., Robertson, A., Donnelly, C.A., Parry, J.E. (2019). Assessing effects from four years of industry-led badger culling in England on the incidence of bovine tuberculosis in cattle, 2013–2017. *Scientific Reports* 9(1). DOI: 10.1038/s41598-019-49957-6.

Downs, S. H., Ashfield, S., Arnold, M., Roberts, T., Prosser, A., Robertson, A., Frost, S., Harris, K., Avigad, R., & Smith, G. C. (2022). Detection of a local *Mycobacterium bovis* reservoir using cattle surveillance data. *Transboundary and Emerging Diseases* 69, e104–e118. https://doi.org/10.1111/tbed.14272

Doyle, R., Clegg, T.A., McGrath, G., Tratalos, J., Barrett, D., Lee, A., More, S.J. (2018). The bovine tuberculosis cluster in north County Sligo during 2014-16. Irish Veterinary Journal 71(1). DOI: 10.1186/s13620-018-0135-z.

Doyle, L.P., Courcier, E.A., Gordon, A.W., O'Hagan, M.J.H., Johnston, P., McAleese, E., Buchanan, J.R., Stegeman, J.A., Menzies, F.D. (2020). Northern Ireland Farm

Level Management Factors for Prolonged Bovine Tuberculosis Herd Breakdowns. *Epidemiology and Infection*. DOI: 10.1017/S0950268820002241.

Doyle, L.P., Courcier, E.A., Gordon, A.W., O'Hagan, M.J.H., Johnston, P., McAleese, E., Buchanan, J.R., Stegeman, J.A., Menzies, F.D. (2022). Northern Ireland farm-level management factors for recurrent bovine tuberculosis herd breakdowns. *Epidemiology and Infection* 150. DOI: 10.1017/S0950268822001479.

Doyle, L.P., Gordon, A.W., Molloy, C., O' Hagan, M.J.H., Georgaki, A., Courcier, E.A., Harwood, R.G., Menzies, F.D. (2023). Assessing the impact of a test and vaccinate or remove badger intervention project on bovine tuberculosis levels in cattle herds. *Epidemiology and Infection* 151. DOI: 10.1017/S0950268823001061.

Duault, H., Durand, B., Canini, L. (2024). Outbreak reconstruction with a slowly evolving multi-host pathogen: A comparative study of three existing methods on *Mycobacterium bovis* outbreaks. *Epidemics* 49. DOI:10.1016/j.epidem.2024.100794.

Enticott, G. (2015). Public attitudes to badger culling to control bovine tuberculosis in rural Wales. *European Journal of Wildlife Research* 61(3): 387-398. DOI: 10.1007/s10344-015-0905-9.

Enticott, G., Maye, D., Naylor, R., Brunton, L., Downs, S.H., Donnelly, C.A. (2020). An assessment of risk compensation and spillover behavioural adaptions associated with the use of vaccines in animal disease management. *Vaccine* 38(5): 1065-1075. DOI: 10.1016/j.vaccine.2019.11.037.

Ferreira, E.M., Duarte, E.L., Cunha, M.V., Mira, A., Santos, S.M. (2023). Disentangling wildlife-cattle interactions in multi-host tuberculosis scenarios: systematic review and meta-analysis. *Mammal Review* 53(4): 287-302. DOI: 10.1111/mam.12324.

Fournier, A., Young, I., Rajić, A., Greig, J., Lejeune, J. (2015). Social and Economic Aspects of the Transmission of Pathogenic Bacteria between Wildlife and Food Animals: A Thematic Analysis of Published Research Knowledge. *Zoonoses and Public Health* 62(6): 417-428. DOI: 10.1111/zph.12179.

Garner, R. (2017). Bovine TB, Badger Culling and Applied Ethics: Utilitarianism, Animal Welfare and Rights. *Journal of Agricultural and Environmental Ethics* 30(4): 579-584. DOI: 10.1007/s10806-017-9677-4.

Gaughran, A., Kelly, D.J.,MacWhite, T., Mullen, E., Maher, P., Good, M., Marples, N.M. (2018). Super-ranging. A new ranging strategy in European badgers. *PLoS ONE* 13(2). DOI: 10.1371/journal.pone.0191818.

Gaughran, A., MacWhite, T., Mullen, E., Maher, P., Kelly, D.J., Good, M., Marples, N.M. (2019). Dispersal patterns in a medium-density Irish badger population: Implications for understanding the dynamics of tuberculosis transmission. *Ecology and Evolution* 9(23): 13142-13152. DOI: 10.1002/ece3.5753.

Gaughran, A., Mullen, E., MacWhite, T., Maher, P., Kelly, D.J., Kelly, R., Good, M. Marples, N.M. (2021). Badger territoriality maintained despite disturbance of major road construction. *PLoS ONE* 16(9 September). DOI: 10.1371/journal.pone.0242586.

Godfray, H. C. J., Donnelly, C. A., Kao, R. R., Macdonald, D. W., McDonald, R. A., Petrokofsky, G., Wood, J. L. N., Woodroffe, R., Young, D. B., McLean, A. (2013). A restatement of the natural science evidence base relevant to the control of bovine tuberculosis in Great Britain. *Proc Biol Sci* 280(1768): 20131634. doi: 10.1098/rspb.2013.1634.

Godfray, C., Donnelly, C., Hewinson, G., Winter, M., Wood, J. (2018). Bovine TB strategy review Report to Rt Hon Michael Gove MP, Secretary of State, Department for Environment, Food and Rural Affairs.

Gormley, E., Bhuachalla, D.N., O'Keeffe, J., Murphy, D., Aldwell, F.E., Fitzsimons, T., Stanley, P., Tratalos, J.A., McGrath, G., Fogarty, N., Kenny, K., More, S.J., Messam, L.L.M., Corner, L.A.L. (2017). Oral vaccination of free-living badgers (*Meles meles*) with Bacille Calmette Guérin (BCG) vaccine confers protection against tuberculosis. *PLoS ONE* 12(1). DOI: 10.1371/journal.pone.0168851.

Gormley, E., Corner, L.A.L. (2018). Wild Animal Tuberculosis: Stakeholder Value Systems and Management of Disease. *Frontiers in Veterinary Science* 5. DOI: 10.3389/fvets.2018.00327.

Gormley, E., Ní Bhuachalla, D., Fitzsimons, T., O'Keeffe, J., McGrath, G., Madden, J.M., Fogarty, N., Kenny, K., Messam, L.L.M., Murphy, D., Corner, L.A.L. (2022). Protective immunity against tuberculosis in a free-living badger population vaccinated orally with Mycobacterium bovis Bacille Calmette–Guérin. *Transboundary and Emerging Diseases* 69(4): e10-e19. DOI: 10.1111/tbed.14254.

Gortazar, C., Diez-Delgado, I., Barasona, J.A., Vicente, J., De La Fuente, J., Boadella, M. (2015a). The wild side of disease control at the wildlife-livestock-human interface: a review. *Frontiers in Veterinary Science* 2. DOI: 10.3389/fvets.2014.00027.

Gortázar, C., Amat, A.C., O'Brien, D.J. (2015b). Open questions and recent advances in the control of a multi-host infectious disease: animal tuberculosis. *Mammal Review* 45(3): 160-175. DOI: 10.1111/mam.12042.

Gowtage, S., Williams, G.A., Henderson, R., Aylett, P., MacMorran, D., Palmer, S., Robertson, A., Lesellier, S., Carter, S.P., Chambers, M.A. (2017). Testing of a palatable bait and compatible vaccine carrier for the oral vaccination of European badgers (Meles meles) against tuberculosis. *Vaccine* 35(6): 987-992. DOI: 10.1016/j.vaccine.2016.12.004.

Ham, C., Donnelly, C.A., Astley, K.L., Jackson, S.Y.B., Woodroffe, R. (2019). Effect of culling on individual badger *Meles meles* behaviour: Potential implications for bovine tuberculosis transmission. *Journal of Applied Ecology* 56(11): 2390-2399. DOI: 10.1111/1365-2664.13512.

Hamilton, L., Evans, N., Allcock, J. (2019). “I don't go to Meetings": understanding farmer perspectives on bovine TB and biosecurity training. *Veterinary Record* 184, 410. https://doi.org/10.1136/vr.104995

Hayes, B.H., Vergne, T., Andraud, M., Rose, N. (2023). Mathematical modeling at the livestock-wildlife interface: scoping review of drivers of disease transmission between species. *Frontiers in Veterinary Science* 10. DOI: 10.3389/fvets.2023.1225446.

Herrero-García, G., Vaz-Rodrigues, R., Pozo, P., Barroso, P., Relimpio, D., Nácar, J., Grau, A., Mínguez, O., García-Rodríguez, A., Balseiro, A., Gortázar, C. (2024). Farm management practices and host species richness associated with higher likelihood of tuberculosis positive farms in Western Spain. *European Journal of Wildlife Research* 70(4). DOI: 10.1007/s10344-024-01833-z.

Houtsma, E., Clegg, T.A., Good, M., More, S.J. (2018). Further improvement in the control of bovine tuberculosis recurrence in Ireland. *Veterinary Record* 183, no. 20 (2018): 622-622.

Jolma, E. R., Delahay, R.J., Smith, F., Drewe, J.A. (2022). Serologic responses correlate with current but not future bacterial shedding in badgers naturally infected with *Mycobacterium bovis*. *Transboundary and Emerging Diseases* 69(4): 1922-1932. DOI: 10.1111/tbed.14181.

Juste, R. A., Blanco-Vázquez, C., Barral, M., Prieto, J.M., Varela-Castro, L., Lesellier, S., Dave, D., Sevilla, I.A., Martín Ezquerra, A.B., Adriaensen, H., Herrero-García, G., Garrido, J.M., Casais, R., Balseiro, A. (2023). Efficacy of heat-inactivated Mycobacterium bovis vaccine delivered to European badgers (*Meles meles*) through edible bait. *Heliyon* 9(9). DOI: 10.1016/j.heliyon.2023.e19349.

Keenan, C., Saunders, C., Price, S., Hinchliffe, S., McDonald, R.A. (2020). From Conflict to Bridges: Towards Constructive Use of Conflict Frames in the Control of Bovine Tuberculosis. *Sociologia Ruralis* 60(2): 482-504. DOI: 10.1111/soru.12290.

Kelly, D.J., Gaughran, A., Mullen, E., MacWhite, T., Maher, P., Good, M., Marples, N.M. (2020). Extra territorial excursions by European badgers are not limited by age, sex or season. *Scientific Reports*, vol. 10, Article ID 9665.

Kelly, D.J., Mullen, E., Good, M. (2021). Bovine Tuberculosis: The Emergence of a New Wildlife Maintenance Host in Ireland. *Frontiers in Veterinary Science* 8. DOI: 10.3389/fvets.2021.632525.

Konzen, E., Delahay, R.J., Hodgson, D.J., McDonald, R.A., Pollock, E.B., Spencer, S.E.F., McKinley, T.J. (2024). Efficient modelling of infectious diseases in wildlife: A case study of bovine tuberculosis in wild badgers. *PLoS Computational Biology* 20(11 November). DOI: 10.1371/journal.pcbi.1012592

Langton, T.E.S., Jones, M.W., McGill, I. (2022). Analysis of the impact of badger culling on bovine tuberculosis in cattle in the high-risk area of England, 2009–2020. *Veterinary Record* 190(6). DOI: 10.1002/vetr.1384.

Lederman, Z. (2016). One health and culling as a public health measure. *Public Health Ethics* 9(1): 5-23. DOI: 10.1093/phe/phw002.

Lederman, Z., Magalhaes-Sant'Ana, M., Voo, T.C. (2021). Stamping Out Animal Culling: From Anthropocentrism to One Health Ethics. *Journal of Agricultural & Environmental Ethics* 34(5). DOI: 10.1007/s10806-021-09868-x.

Lesellier, S., Boschiroli, M.L., Barrat, J., Wanke, C., Salguero, F.J., Garcia-Jimenez, W.L., Nunez, A., Godinho, A., Spiropoulos, J., Palmer, S., Dave, D. Anderson, P., Boucher, J.M., de Cruz, K, Henault, S., Michelet, L., Gowtage, S., Williams, G.A., Nadian, A.K., Monchatre-Leroy, E., Boue, F., Chambers, M.A., Richomme, C. (2019). Detection of live M. bovis BCG in tissues and IFN-gamma responses in European badgers (Meles meles) vaccinated by oropharyngeal instillation or directly in the ileum. *BMC veterinary research* 15(1): 445. DOI: 10.1186/s12917-019-2166-4.

Lesellier, S., Birch, C.P.D, Davé, D., Dalley, D., Gowtage, S., Palmer, S., McKenna, C., Williams, G.A., Ashford, R., Weyer, U., Beatham, S., Coats, J., Nunez, A., Sanchez-Cordon, P., Spiropoulos, J., Powell, S., Sawyer, J., Pascoe, j., Hendon-Dunn, C., Bacon, J., Chambers, M.A. (2020). Bioreactor-grown bacillus of calmette and guérin (BCG) vaccine protects badgers against virulent *mycobacterium bovis* when administered orally: Identifying limitations in baited vaccine delivery." *Pharmaceutics* 12(8): 1-22. DOI: 10.3390/pharmaceutics12080782.

Magowan, E. A., Maguire, I.E., Smith, S., Redpath, S., Marks, N.J., Wilson, R.P., Menzies, F., O'Hagan, M., Scantlebury, D.M. (2022). Dead-reckoning elucidates fine-scale habitat use by European badgers (*Meles meles*). *Animal Biotelemetry* 10(1). DOI: 10.1186/s40317-022-00282-2.

Martin, L.E.R., Byrne, A.W., O'Keeffe, J., Miller, M.A., Olea-Popelka, F.J. (2017). Weather influences trapping success for tuberculosis management in European badgers (*Meles meles*). *European Journal of Wildlife Research* 63(1). DOI: 10.1007/s10344-017-1089-2.

Martin, S. W., O'Keeffe, J., Byrne, A.W., Rosen, L.E., White, P.W., McGrath, G. (2020). Is moving from targeted culling to BCG-vaccination of badgers (*Meles meles*) associated with an unacceptable increased incidence of cattle herd tuberculosis in the Republic of Ireland? A practical non-inferiority wildlife intervention study in the Republic of Ireland (2011-2017). *Preventive Veterinary Medicine* 179. DOI: 10.1016/j.prevetmed.2020.105004.

Maye, D., Enticott, G., Naylor, R. (2017). Using scenario-based influence mapping to examine farmers' biosecurity behaviour. *Land Use Policy* 66: 265-277. DOI: 10.1016/j.landusepol.2017.04.026.

Maye, D., Enticott, G., Naylor, R. (2020). Theories of Change in Rural Policy Evaluation. *Sociologia Ruralis* 60(1): 198-221. DOI: 10.1111/soru.12269.

McClune, D.W., Marks, N.J., Delahay, R.J., Montgomery, W.I., Scantlebury, D.M. (2015). Behaviour-time budget and functional habitat use of a free-ranging European badger(Meles meles). *Animal Biotelemetry* 3(1). DOI: 10.1186/s40317-015-0025-z.

McCormack, J. (2023). Horizon scanning: what next for bovine TB control in England? *Irish Veterinary Journal* 76(Suppl 1): 18. DOI: 10.1186/s13620-023-00242-z.

McCulloch, S.P., Reiss, M.J (2017a). The Development of an Animal Welfare Impact Assessment (AWIA) Tool and Its Application to Bovine Tuberculosis and Badger Control in England. *Journal of Agricultural and Environmental Ethics* 30(4): 485-510. DOI: 10.1007/s10806-017-9684-5.

McCulloch, S.P., Reiss, M.J. (2017b). Bovine Tuberculosis and Badger Control in Britain: Science, Policy and Politics. *Journal of Agricultural and Environmental Ethics* 30(4): 469-484. DOI: 10.1007/s10806-017-9686-3.

McCulloch, S.P., Reiss, M.J. (2017c). Bovine Tuberculosis and Badger Culling in England: An Animal Rights-Based Analysis of Policy Options. *Journal of Agricultural and Environmental Ethics* 30(4): 535-550. DOI: 10.1007/s10806-017-9685-4.

McCulloch, S.P., Reiss, M.J. (2017d). Bovine Tuberculosis Policy in England: Would a Virtuous Government Cull Mr Badger? *Journal of Agricultural and Environmental Ethics* 30(4): 551-563. DOI: 10.1007/s10806-017-9687-2.

McCulloch, S.P., Reiss, M.J. (2017e). Bovine Tuberculosis and Badger Culling in England: A Utilitarian Analysis of Policy Options. *Journal of Agricultural and Environmental Ethics* 30(4): 511-533. DOI: 10.1007/s10806-017-9680-9.

McCulloch, S.P., Reiss, M.J (2018). A proposal for a UK Ethics Council for animal policy: The case for putting ethics back into policy making. *Animals* 8(6). DOI: 10.3390/ani8060088.

McGill, K., Fitzsimons, T., Duignan, A., Corner, L., Lesellier, S., Gormley, E. (2022). Seroconversion against antigen MPB83 in badgers (*Meles meles*) vaccinated with multiple doses of BCG strain Sofia. *Research in Veterinary Science* 149: 119-124. DOI: 10.1016/j.rvsc.2022.06.011.

Menzies, F.D., McCormick, C.M., O'Hagan, M.J.H., Collins, S.F., McEwan, J., McGeown, C.F., McHugh, G.E., Hart, C.D., Stringer, L.A., Molloy, C., Burns, G., McBride, S.J., Doyle, L.P., Courcier, E.A., McBride, K.R., McNair, J., Thompson, S., Corbett, D.M., Harwood, R.G., Trimble, N.A. (2021). Test and vaccinate or remove: Methodology and preliminary results from a badger intervention research project. *Veterinary Record* 189(5): no. DOI: 10.1002/vetr.248.

Miguel, E., Grosbois, V., Caron, A., Pople, D., Roche, B., Donnelly, C.A. (2020). A systemic approach to assess the potential and risks of wildlife culling for infectious disease control. *Communications Biology* 3(1). DOI: 10.1038/s42003-020-1032-z.

Mills, C. L., Woodroffe, R., Donnelly, C.A. (2024a). An extensive re-evaluation of evidence and analyses of the Randomised Badger Culling Trial (RBCT) I: Within proactive culling areas. *Royal Society Open Science* 11(8). DOI: 10.1098/rsos.240385.

Mills, C. L., Woodroffe, R., Donnelly, C.A. (2024b). An extensive re-evaluation of evidence and analyses of the Randomised Badger Culling Trial II: In neighbouring areas. *Royal Society Open Science* 11(8). DOI: 10.1098/rsos.240386.

Milne, G., Allen, A., Graham, J., Lahuerta-Marin, A., McCormick, C., Presho, E., Reid, N., Skuce, R., Byrne, A.W. (2020). Bovine tuberculosis breakdown duration in cattle herds: An investigation of herd, host, pathogen and wildlife risk factors. *PeerJ* 2020(2). DOI: 10.7717/peerj.8319.

More, S.J., Good, M. (2015). Understanding and managing bTB risk: Perspectives from Ireland. *Veterinary Microbiology* 176(3-4): 209-218. DOI: 10.1016/j.vetmic.2015.01.026.

More, S.J. (2019). Can bovine TB be eradicated from the Republic of Ireland? Could this be achieved by 2030? *Irish veterinary journal* 72: 3. DOI: 10.1186/s13620-019-0140-x.

Moustakas, A., Evans, M.R. (2015). Coupling models of cattle and farms with models of badgers for predicting the dynamics of bovine tuberculosis (TB). *Stochastic Environmental Research and Risk Assessment* 29(3): 623-635. DOI: 10.1007/s00477-014-1016-y.

Mullen, E.M., MacWhite, T., Maher, P.K., Kelly, D.J., Marples, N.M., Good, M. (2015). The avoidance of farmyards by European badgers *Meles meles* in a medium density population. *Applied Animal Behaviour Science* 171: 170-176. DOI: 10.1016/j.applanim.2015.08.021.

Murphy, A.R.J., Travis, E.R., Hibberd, V., Porter, D., Wellington, E.M.H. (2020). Evaluation of a Fecal Shedding Test To Detect Badger Social Groups Infected with *Mycobacterium bovis*. *Journal of clinical microbiology* 59(1). DOI: 10.1128/jcm.01226-20.

Naylor, R., Manley, W., Maye, D., Enticott, G.,Ilbery, B., Hamilton-Webb, A. (2017). The Framing of Public Knowledge Controversies in the Media: A Comparative Analysis of the Portrayal of Badger Vaccination in the English National, Regional and Farming Press. *Sociologia Ruralis* 57(1): 3-22. DOI: 10.1111/soru.12105.

Ni Bhuachalla, D., Corner, L.A., More, S.J., Gormley, E. (2015). The role of badgers in the epidemiology of *Mycobacterium bovis* infection (tuberculosis) in cattle in the United Kingdom and the Republic of Ireland: current perspectives on control strategies. *Veterinary medicine* 6: 27-38. DOI: 10.2147/vmrr.S53643.

O'Hagan, M.J.H., Matthews, D.I., Laird, C., McDowell, S.W.J. (2016). Farmers' beliefs about bovine tuberculosis control in Northern Ireland. *Veterinary Journal* 212: 22-26. DOI: 10.1016/j.tvjl.2015.10.038.

O'Hagan, M.J.H., McCormick, C.M., Collins, S.F., McBride, K.R., Menzies, F.D. (2021a). Are major roads effective barriers for badger (*Meles meles*) movements? *Research in Veterinary Science* 138: 49-52. DOI: 10.1016/j.rvsc.2021.06.003.

O'Hagan, M.J.H., Gordon, A.W., McCormick, C.M., Collins, S.F., Trimble, N.A., McGeown, C.F., McHugh, G.E., McBride, K.R., Menzies, F.D. (2021b). Effect of selective removal of badgers (*Meles meles*) on ranging behaviour during a 'Test and Vaccinate or Remove' intervention in Northern Ireland. *Epidemiology and Infection* 149. DOI: 10.1017/S0950268821001096.

O'Hare, A., Balaz, D., Wright, D.M., McCormick, C., McDowell, S., Trewby, H., Skuce, R.A., Kao, R.R. (2021). A new phylodynamic model of *Mycobacterium bovis* transmission in a multi-host system uncovers the role of the unobserved reservoir. PLoS Computational Biology 17(6). DOI: 10.1371/journal.pcbi.1009005.

Palphramand, K., Delahay, R., Robertson, A., Gowtage, S., Williams, G.A. McDonald, R.A., Chambers, M., Carter, S.P. (2017). Field evaluation of candidate baits for oral delivery of BCG vaccine to European badgers, *Meles meles. Vaccine* 35(34): 4402-4407. DOI: 10.1016/j.vaccine.2017.06.059.

Payne, A., Ruette, S., Jacquier, M., Richomme, C., Lesellier, S., Middleton, S., Duhayer, J., Rossi, S. (2022). Estimation of Bait Uptake by Badgers, Using Non-invasive Methods, in the Perspective of Oral Vaccination Against Bovine Tuberculosis in a French Infected Area. *Frontiers in Veterinary Science* 9. DOI: 10.3389/fvets.2022.787932.

Perrett, S., Lesellier, S., Rogers, F., Williams, G.A., Gowtage, S., Palmer, S., Dalley, D., Davé, D., Weyer, U., Wood, E., Salguero, F.J., Nunez, A., Reed, N., Chambers, M.A. (2018). Assessment of the safety of Bacillus Calmette-Guérin vaccine administered orally to badgers (*Meles meles*). *Vaccine* 36(15): 1990-1995. DOI: 10.1016/j.vaccine.2018.02.101.

Phoenix, J. (2024). How can we do ethnographic research in a controversy? Lessons and reflections from a multi-sided ethnography of badger culling and bovine Tuberculosis. *Qualitative Research.* DOI: 10.1177/14687941241234287.

Prentice, J. C., Fox, N.J., Hutchings, M.R., White, P.C.L., Davidson, R.S., Marion, G. (2019). When to kill a cull: Factors affecting the success of culling wildlife for disease control. *Journal of the Royal Society Interface* 16(152). DOI: 10.1098/rsif.2018.0901.

Price, S., Saunders, C., Hinchliffe, S., McDonald, R.A. (2017). From contradiction to contrast in a countryside conflict: Using Q Methodology to reveal a diplomatic space for doing TB differently. *Environment and Planning* A 49(11): 2578-2594. DOI: 10.1177/0308518X17726782.

Redpath, S. H. A., Marks, N.J., Menzies, F.D., O'Hagan, M.J.H., Wilson, R.P., Smith, S., Magowan, E.A., McClune, D.W., Collins, S.F., McCormick, C.M., Scantlebury, D.M. (2023). Impact of test, vaccinate or remove protocol on home ranges and nightly movements of badgers a medium density population. *Scientific Reports* 13(1). DOI: 10.1038/s41598-023-28620-1.

Reis, A. C., Ramos, B., Pereira, A.C., Cunha, M.V. (2021). The hard numbers of tuberculosis epidemiology in wildlife: A meta-regression and systematic review. Transboundary and Emerging Diseases 68(6): 3257-3276. DOI: 10.1111/tbed.13948.

Réveillaud, É., Desvaux, S., Boschiroli, 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. doi: 10.3389/fvets.2018.00262

Robertson, A., Chambers, M.A., Delahay, R. J., McDonald, R.A., Palphramand, K.L., Rogers, F., Carter, S.P. (2015). Exposure of nontarget wildlife to candidate TB vaccine baits deployed for European badgers. *European Journal of Wildlife Research* 61(2): 263-269. DOI: 10.1007/s10344-014-0896-y.

Robertson, A., Delahay, R. J., McDonald, R.A., Aylett, P., Henderson, R., Gowtage, S., Chambers, M.A., Carter, S.P. (2016). Behaviour of European badgers and non-target species towards candidate baits for oral delivery of a tuberculosis vaccine. *Preventive Veterinary Medicine* 135: 95-101. DOI: 10.1016/j.prevetmed.2016.11.007.

Robertson, A., Delahay, R.J., Wilson, G.J., Vernon, I.J., McDonald, R.A., Judge, J. (2017). How well do farmers know their badgers? Relating farmer knowledge to ecological survey data. *The Veterinary record* 180(2): 48. DOI: 10.1136/vr.103819.

Robertson, A., Judge, J., Wilson, G.J., Vernon, I.J., Delahay, R.J., McDonald, R.A. (2019). Predicting badger visits to farm yards and making predictions available to farmers. *PloS one* 14(5): e0216953. DOI: 10.1371/journal.pone.0216953.

Robertson, A., Palphramand, K.L., McDonald, R.A., Middleton, S., Chambers, M.A., Delahay, R.J., Carter, S.P. (2022). Uptake of baits by wild badgers: Influences of deployment method, badger age and activity patterns on potential delivery of an oral vaccine. *Preventive Veterinary Medicine* 206. DOI: 10.1016/j.prevetmed.2022.105702.

Robinson, P.A., Corner, L.A.L., Courcier, E.A., McNair, J., Artois, M., Menzies, F.D., Abernethy, D.A. (2012). BCG vaccination against tuberculosis in European badgers (Meles meles): a review. *Comparative Immunology, Microbiology and Infectious Diseases* 35, 277–287. (doi:10.1016/j.cimid.2012.01.009)

Robinson, P.A. (2019). Performativity and a microbe: Exploring *Mycobacterium bovis* and the political ecologies of bovine tuberculosis. *Biosocieties* 14(2): 179-204. DOI: 10.1057/s41292-018-0124-1.

Rosen, L.E., Fogarty, U., O'Keeffe, J.J., Olea-Popelka, F.J. (2019). Monitoring European badger (*Meles meles*) reproduction under evolving bovine tuberculosis management in Ireland. *European Journal of Wildlife Research* 65(6). DOI: 10.1007/s10344-019-1340-0.

Ross, J.B.G., Newman, C., Buesching, C.D., Macdonald, D.W. (2022). Preserving identity in capture-mark-recapture studies: increasing the accuracy of minimum number alive (MNA) estimates by incorporating inter-census trapping efficiency variation. *Mammalian Biology* 102(3): 567-580. DOI: 10.1007/s42991-021-00210-6.

Rossi, G., Crispell, J., Brough, T., Lycett, S.J., White, P.C.L., Allen, A., Ellis, R.J., Gordon, S.V., Harwood, R., Palkopoulou, E., Presho, E.L., Skuce, R., Smith, G.C., Kao, R.R. (2022). Phylodynamic analysis of an emergent Mycobacterium bovis outbreak in an area with no previously known wildlife infections. *Journal of Applied Ecology* 59(1): 210-222. DOI: 10.1111/1365-2664.14046.

Ryan, E., Breslin, P., O'Keeffe, J., Byrne, A.W., Wrigley, K., Barrett, D. (2023). The Irish bTB eradication programme: combining stakeholder engagement and research-driven policy to tackle bovine tuberculosis. *Irish Veterinary Journal* 76(SUPPL 1). DOI: 10.1186/s13620-023-00255-8.

Schreiner, C.L., Nuismer, S.L., Basinski, A.J. (2020). When to vaccinate a fluctuating wildlife population: Is timing everything? *Journal of Applied Ecology* 57(2): 307-319. DOI: 10.1111/1365-2664.13539.

Smith, C.M., Downs, S.H., Mitchell, A., Hayward, A.C., Fry, H., Comber, S.C.L. (2015). Spatial targeting for bovine tuberculosis control: Can the locations of infected cattle be used to find infected badgers? *PLoS ONE* 10(11). DOI: 10.1371/journal.pone.0142710.

Smith, G. C., Delahay, R.J., McDonald, R.A., Budgey, R. (2016). Model of selective and non-selective management of badgers (*Meles meles*) to control bovine tuberculosis in badgers and cattle. *PLoS ONE* 11(11). DOI: 10.1371/journal.pone.0167206.

Smith, G.C., Delahay, R.J. (2018). Modeling as a Decision Support Tool for Bovine TB Control Programs in Wildlife. *Frontiers in veterinary science* 5: 276. DOI: 10.3389/fvets.2018.00276.

Smith, F., Robertson, A., Smith, G.C., Gill, P., McDonald, R.A., Wilson, G., Delahay, R.J. (2020). Estimating wildlife vaccination coverage using genetic methods. *Preventive Veterinary Medicine* 183. DOI: 10.1016/j.prevetmed.2020.105096.

Smith, F., Rogers, F., Tomlinson, A., Arnold, L., Benton, C., Spyvee, P., Boxall, S., Whiteside, J., Delahay, R. (2021). A novel approach for trap-side restraint and blood sampling in European badgers. *European Journal of Wildlife Research* 67(5). DOI: 10.1007/s10344-021-01520-3.

Smith, G.C., Budgey, R. (2021). Simulating the next steps in badger control for bovine tuberculosis in England. *PLoS ONE* 16(3 March). DOI: 10.1371/journal.pone.0248426.

Smith, G. C., Brough, T., Podgórski, T., Ježek, M., Šatrán, P., Vaclavek, P., Delahay, R. (2022a). Defining and testing a wildlife intervention framework for exotic disease control. *Ecological Solutions and Evidence* 3(4). DOI: 10.1002/2688-8319.12192.

Smith, G. C., Barber, A., Breslin, P., Birch, C., Chambers, M., Dave, D., Hogarth, P., Gormley, E., Lesellier, S., Balseiro, A., Budgey, R. (2022b). Simulating partial vaccine protection: BCG in badgers. *Preventive Veterinary Medicine* 204. DOI: 10.1016/j.prevetmed.2022.105635.

Stanyer, J. (2021). Biased or balanced? Assessing BBC news and current affairs performance in covering the badger cull in England. *Journal of Rural Studies* 81: 59-67. DOI: 10.1016/j.jrurstud.2020.11.011.

Thomas, J., Balseiro, A., Gortazar, C., Risalde, M.A. (2021). Diagnosis of tuberculosis in wildlife: a systematic review. *Veterinary research* 52(1): 31. DOI: 10.1186/s13567-020-00881-y.

Tomlinson, A. J., Chambers, M.A., McDonald, R.A., Delahay, R.J. (2015). Association of quantitative interferon-γ responses with the progression of naturally acquired *Mycobacterium bovis* infection in wild European badgers (*Meles meles*). *Immunology* 144(2): 263-270. DOI: 10.1111/imm.12369.

Torgerson, P. R., Hartnack, S., Rasmussen, P., Lewis, F., Langton, T.E.S. (2024). Absence of effects of widespread badger culling on tuberculosis in cattle. *Scientific Reports* 14(1). DOI: 10.1038/s41598-024-67160-0.

Tratalos, J., Madden, J., McGrath, G., More, S. (2024). Computing metrics to inform selection of candidate areas for a regionalized approach to bovine tuberculosis eradication in Ireland. *Veterinaria Italiana* 60(4 Special Issue). DOI: 10.12834/VetIt.3486.23927.2.

Ward, C. V., Heydon, M., Lakin, I., Sullivan, A.J., Siriwardena, G.M. (2022). Breeding bird population trends during 2013–2019 inside and outside of European badger control areas in England. *Journal of Zoology* 318(3): 166-180. DOI: 10.1111/jzo.13010.

White, L. A., Forester, J.D., Craft, M.E. (2018). Dynamic, spatial models of parasite transmission in wildlife: Their structure, applications and remaining challenges. *Journal of Animal Ecology* 87(3): 559-580. DOI: 10.1111/1365-2656.12761.

Woodroffe, R., Donnelly, C.A., Ham, C., Jackson, S.Y.B., Moyes, K., Chapman, K., Stratton, N.G., Cartwright, S.J. (2016). Badgers prefer cattle pasture but avoid cattle: implications for bovine tuberculosis control. *Ecology Letters* 19(10): 1201-1208. DOI: 10.1111/ele.12654.

Woodroffe, R., Donnelly, C.A., Ham, C., Jackson, S.Y.B., Moyes, K., Chapman, K., Stratton, N.G., Cartwright, S.J. (2017). Ranging behaviour of badgers *Meles meles* vaccinated with Bacillus Calmette Guerin. *Journal of Applied Ecology* 54(3): 718-725. DOI: 10.1111/1365-2664.12837.

Woodroffe, R., Donnelly, C.A., Chapman, K., Ham, C., Moyes, K., Stratton, N.G., Cartwright, S.J. (2021). Successive use of shared space by badgers and cattle: implications for *Mycobacterium bovis* transmission. *Journal of Zoology* 314(2): 132-142. DOI: 10.1111/jzo.12863.

Woodroffe, R.,K. Astley, A., Barnecut, R., Brotherton, P.N.M., Donnelly, C.A., Grub, H.M.J., Ham, C., Howe, C., Jones, C., Marriott, C., Miles, V., Rowcliffe, M., Shelley, T., Truscott, K. (2024). Farmer-led badger vaccination in Cornwall: Epidemiological patterns and social perspectives. *People and Nature* 6(5): 1960-1973. DOI: 10.1002/pan3.10691.

Wright, D.M., Reid, N., Montgomery, W.I., Allen, A.R., Skuce, R.A., Kao, R.R. (2015). Herd-level bovine tuberculosis risk factors: Assessing the role of low-level badger population disturbance. *Scientific Reports* 5. DOI: 10.1038/srep13062.

Abbreviations

Abbreviated term	*Full name*
BCG	Bacillus Calmette-Guérin
BCP	Badger Control Policy (in England)
bTB	Bovine tuberculosis
BVDP	Badger Vaccine Deployment Project
CI	Confidence Interval
CrI	Credibility Interval
DAERA	Department of Agriculture Environment and Rural Affairs
DIVA test	Differentiating Infected from Vaccinated Animals (test)
DPP	Dual Path Platform (test)
FMD	Foot and Mouth Disease
GB	Great Britain
HIMB	Heat-inactivated (dead) *M. bovis* vaccines
IAA	Intensive Action Area (in Wales)
IFNg	Interferon Gamma (test)
IRR	Incidence Rate Ratio
M. bovis	*Mycobacterium bovis*
NI	Northern Ireland
OTF	Official Tuberculosis Free Status
OTFS	Official Tuberculosis Free Status Suspended
OTFW	Official Tuberculosis Free Status Withdrawn
PCR	Polymerase Chain Reaction
RBCT	Randomised Badger Culling Trial
ROI	Republic of Ireland
TBSPG	Tuberculosis Strategic Partnership Group
TVR	Test and Vaccinate or Remove
WGS	Whole Genomic Sequencing
WOAH	World Organisation for Animal Health (formerly OIE)

Glossary

Technical term	*Term definition/explanation*
Amplification and feedback from the other host species	Where an infection such as *M. bovis* is present in different reservoir hosts and infection in one species is dependent upon multiplication (amplification) of the infection within another species along with transfer of the infection back (feedback) to the other species.
Bayesian model	Statistical models specify a set of statistical assumptions and processes that represent how the sample data are generated. In Bayesian models, prior assumptions/distributions can be included thus informing the model using previously known information. Prior information is not included in frequentist models.
Bayesian phylogenetics	Bayesian is a specific branch of statistics that can use prior information to inform the outcome of a statistical analysis. Phylogenetics is a tree type structure formed using techniques that map the genetic relationships between different isolates of an organism (e.g. *M. bovis*). The tree highlights the ancestral relationships between the isolates.
Biological cause–effect relationship	With respect to infectious diseases such as TB (mainly caused by *M. bovis* infection) the agent (*M. bovis*) has to be demonstrated as present or introduced before the disease can occur. In other words, for a biological link to be established, the cause/infectious agent must be observed before the effect of infection is observed.
Buffer zone incidence rate	The rate at which new cases/incident are observed over a time period within an area that lies between an intervention area and an area outside of the defined buffer zone.
Compartmental	In modelling terms of infectious diseases, a compartmental model places animals within a population within one of the model's categories. For example, animals can be susceptible to infection (S), infected (I) or resistant to infection (R); sometimes called a SIR model.
95% Confidence Interval [CI]	The range of values (upper and lower) that you can be 95% certain contains the true mean/average of the population being studied. In other words, 95% of the time the true average within the study group will appear within the range of values presented. Confidence intervals are used when representing classical/frequentist statistical outputs.

95% credibility interval [CrI]	As for the definition given for 95% confidence intervals but credibility interval is the term used when Bayesian statistical methods employed.
Convenience sample	Convenience sampling (also known as grab sampling, accidental sampling, or opportunity sampling) is a type of non-probability sampling that involves the sample being drawn from that part of the population that is close to hand and may not be representative of the population.
Epidemiology	The study of patterns, causes, and effects of health and disease conditions in defined populations.
Environmental shedding	With respect to *M. bovis* infected animals, environmental shedding refers to the contamination of the infected animals' surroundings through excretion of the infectious agent e.g. in nasal or oral excretions or discharges from abscesses or in faeces or urine.
Fur-clips	When working with wildlife, animals are sometimes marked in an obvious way so as an observer will know the animal has already been captured and processed. Clipping of an area of fur offers one temporary method of identification although it does not distinctly identify individual animals.
Heterogeneity	The quality or state of being diverse in character or content. Significant/increased variability in a specific characteristic of a population or area. Opposite of homogeneity.
Homogeneity	The quality or state of being all the same or all the same kind. There is little variability in a specific characteristic of a population or area. Opposite of heterogeneity.
Incidence	In relation to disease, incidence is the rate of new cases of a disease occurring in a specific population over a particular time-period.
Monthly home range size	In relation to badgers, this represents the land area over which a badger will normally be resident during a month.
Non-specific test cross reactions	Non-specific cross reactivity of an observed agent which initiates reactions outside the main reaction expected. This has implications for any kind of test, including diagnostic tests, and can be a cause of false positives.
Pathogenesis	The manner or process of development of a disease.

Perturbation	A perturbation of a biological system is an alteration of function, induced by external or internal mechanisms. In relation to badgers, this is a change in ranging behaviour caused by changes in the population structure e.g. through badger deaths
R Value	Reproductive value. The effective reproductive number (R) is the average number of secondary cases per infectious case in a population made up of both susceptible and non-susceptible hosts. If $R>1$, the number of cases will increase, such as at the start of an epidemic. Where $R=1$, the disease is endemic, and where $R<1$ there will be a decline in the number of cases.
(test) Sensitivity	Sensitivity (true positive rate) is the probability of a positive test result, conditioned on the individual truly being positive. It is represented by the number of truly infected animals that test positive divided by the total number of truly infected animals that were tested.
Sentinel badgers	In this context, these were BCG vaccinated badgers that were otherwise free of *M. bovis* infection, which were placed with *M. bovis* infected badgers to see if they developed infection.
Serological (tests)	Serology is the scientific study of serum and other body fluids. Serological tests detect/measure the humoral (antibody) response to a specific antigen. The presence of antibodies may indicate exposure to an infectious organism (either through infection or vaccination. An antigen is a toxin or other foreign substance which induces an immune response in the body. Some serological tests allow for the detection of infection rather than vaccination (so called DIVA tests; Differentiating Infected from Vaccinated Animals).
(test) Specificity	Specificity (true negative rate) is the probability of a negative test result, conditioned on the individual truly being negative.
Severity scores	In this context, a predefined scoring system that enabled quantification of the severity of lesions to be given to badgers with *M. bovis* infection was used. These numeric values across the different badger populations could then be compared using statistical analysis
Stat-Pak test	Serological test for the detection of *M. bovis* antibodies using a lateral flow device (like the test-kits used for COVID-19 testing). A precursor to the DPP test, which works using broadly similar technology.
Sterile immunity	Sterile immunity is where the immune system can stop a pathogen, including viruses, from replicating within your body.

Temporal extent (of the culling)	The length of time an activity (culling) is carried out.
Temporal trend	The change in infection rates (or other observed data points) over time or related to the passing of time.
Prevalence	In relation to disease, prevalence is the number of cases of a disease in a specific population at a particular timepoint (point prevalence) or over a specified time-period (period prevalence). Prevalence differs from incidence proportion as prevalence includes all cases (new and pre-existing cases) in the population at the specified time whereas incidence is limited to new cases only.

Annex 1: Detailed methodology

To produce an annotated narrative based on the scientific evidence that were published after the evidence provided in the TBSPG bovine TB eradication strategy (published 15 December 2016[1]), the time period considered was backdated to 1 January 2015 to ensure that no literature was omitted since the TBSPG reported findings. The literature trawl was carried out in early June 2024 so an end date of 31 May 2024 was also set.

An updated scientific literature search was run by AFBI/QUB library on 4 June 2024 based on the following agreed search terms:

(TITLE-ABS-KEY ("bovine tuberculosis" OR "bovine TB" OR "Mycobacterium bovis" OR "tuberculosis" OR “Mycobacterium tuberculosis complex” OR “MTBC”) AND TITLE-ABS-KEY ("intervention*” OR “trial*” OR “vaccin*” OR “BCG” OR “cull*” OR “remov*” OR “control” OR “fertil*”) AND TITLE-ABS-KEY (“badger*” OR “Meles meles”)

AND Publication Year >2014)

AND Peer Reviewed only

Search terms were used in three databases (Web of Science, Scopus (QUB resource) and MEDLINE) and when duplication occurred, the fullest records were kept. Three separate outputs were produced:

- Annotated Style including abstract and an indication of which articles are Open Access.
- Author/Date Style without abstract and including DOI.
- EndNote library

The references obtained from this search were then listed into a spreadsheet and classified as to whether they were considered relevant and acceptable for mention into the annotated bibliography. For example, references were omitted if they were not badger related or were not peer reviewed articles. References were also allocated to one of the following themes so as to broadly group them for inclusion in the annotated text. This grouping did not restrict mention of the paper across other relevant themes.

- Badger ecology
- Badger welfare & ethics
- Badger diagnostics
- Transmission dynamics
- Proactive badger culling
- Reactive badger culling
- Test and vaccinate or remove
- Badger vaccination
- Modelling

[1] TBSPG Bovine TB Eradication Strategy NI | Department of Agriculture, Environment and Rural Affairs (daera-ni.gov.uk)

- Socio-economics
- Miscellaneous

The list of references accepted for inclusion was then circulated to external stakeholders involved with bovine tuberculosis/*M. bovis*/badgers; listed below. These stakeholders were asked to suggest any additional references that were not on this list so as to ensure as full a peer reviewed literature coverage as possible. Returns from the stakeholders were then considered and included where appropriate. For the suggested references not included, a reason was included for its exclusion e.g. outside of date range, not peer reviewed.

- Ulster Farmers Union
- Animal Health and Welfare Northern Ireland
- Northern of Ireland Veterinary Association
- Ulster Wildlife Trust
- Northern Ireland Badger Group
- Council for Nature Conservation and the Countryside
- Holstein UK
- Association of Veterinary Surgeons Practising in Northern Ireland
- National Trust

The search was later extended to cover the period up to 30 November (1 June 2024 to 30 November 2024, inclusive). The resulting search underwent the same processes as previously mentioned.

This process provided a listing of 174 references to be incorporated into the annotated text. The following table provides a summary of the number of references by main theme and country in which the research was related to.

Cross-tabulation showing the number of peer reviewed scientific publications were included in this paper by main theme and by country of origin of the evidence/data

Theme heading	British Isles	France	GB	NI	Non-country specific	Other European	Outside Europe	RoI	Spain	Grand Total
Badger ecology			6	4	2			13		25
Combination - modelled			5	1	2	1		2		11
Cull - proactive			13		2			1		17
Cull - reactive			2					1		3
Diagnostics			8						1	9
Future focus			2	1				4		7
Other		5	1						1	7
Social Science	1		13		3			1		18
Transmission dynamics	2	1	8	5	3			7		26
TVR		1	1	7						9
Vaccination		2	21	1	2		2	6	2	36
Welfare & Ethics			6					1		7
Grand Total	**3**	**9**	**86**	**19**	**14**	**1**	**2**	**36**	**4**	**174**