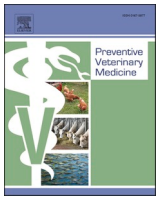
Preventive Veterinary Medicine 238 (2025) 106464

Contents lists available at ScienceDirect

Preventive Veterinary Medicine

journal homepage: www.elsevier.com/locate/prevetmed



Can badger vaccination contribute to bovine TB control? A narrative review of the evidence

Andrew Robertson [a,b,*,1], Mark A. Chambers [c,d], Graham C. Smith [e], Richard J. Delahay [e], Robbie A. McDonald [b], Peter N.M. Brotherton [a]

[a] Natural England, Foss House, Kings Pool, 1-2 Peasholme Green, York, YO17PX, UK
[b] Environment & Sustainability Institute, University of Exeter, Penryn, UK
[c] School of Biosciences and School of Veterinary Medicine, Faculty of Health and Medical Sciences, University of Surrey, Guildford GU2 7XH, UK
[d] Animal and Plant Health Agency, Department of Bacteriology, Addlestone, Surrey, KT153NB, UK
[e] Animal & Plant Health Agency, National Wildlife Management Centre, Sand Hutton, York, YO41 1LZ, UK

ARTICLE INFO

Keywords:
Vaccination
Badger
BCG
Bovine tuberculosis
M. bovis
Wildlife disease

ABSTRACT

In parts of Europe, the European badger *Meles meles* acts as a wildlife host for *Mycobacterium bovis*, the causative agent of bovine tuberculosis (bTB). Options for reducing the risk of transmission of *M. bovis* from badgers to cattle include biosecurity measures, culling, and vaccination of badgers using the BCG vaccine. The use of vaccination as a control measure for tuberculosis (TB) in badgers has increased in recent years, with large-scale deployment in Ireland, and increasing use in England alongside a gradual phasing out of badger culling. Here we review evidence relating to the use of badger vaccination as a tool for controlling TB in badgers and cattle. Vaccination reduces the severity and progression of TB in badgers experimentally infected with *M. bovis* in laboratory studies, and significantly decreases the likelihood of naturally-acquired infection in free-living badgers in field trials. Modelling studies evaluating different strategies for controlling TB in badgers predict that badger vaccination will reduce TB prevalence in badger populations and lead to corresponding reductions in cattle herd disease incidence. While large scale field trials have not been undertaken to quantify the level of impact of badger vaccination on cattle bTB incidence in the UK, field studies in Ireland suggest that in some situations badger vaccination can result in beneficial disease outcomes in cattle which are comparable to those from badger culling. Attitudes to badger vaccination vary among stakeholder groups. Although members of the public are relatively positive about the benefits of vaccination, farmers are generally negative, due to concerns about practicality and effectiveness, along with a view that badger populations need to be controlled. The evidence published to date indicates that badger vaccination has the potential to contribute to the control of TB prevalence in wild badger populations and to form part of a wider strategy for controlling bTB. Future research should focus on investigating the effect of badger vaccination on bTB in cattle, along with understanding the impacts of vaccination in badgers in a broader range of ecological settings. Further understanding of the drivers of negative attitudes towards vaccination will nonetheless be crucial for incentivising and increasing the deployment of badger vaccination.

1. Introduction

Tuberculosis caused by the bacterium *Mycobacterium bovis* has a significant impact on the livestock industry in several countries worldwide (Palmer et al., 2012). The principal livestock host for *M. bovis* is domestic cattle, although the pathogen will also infect a number of other domesticated species including, sheep, pigs, goats and camelids (Broughan et al., 2013). Measures for controlling the prevalence of *M. bovis* in cattle primarily consist of regular diagnostic testing to identify infected individuals or groups, combined with the slaughtering

* Corresponding author at: Natural England, Foss House, Kings Pool, 1-2 Peasholme Green, York, YO17PX, UK.
E-mail addresses: andrew.robertson1@defra.gov.uk (A. Robertson), m.chambers@surrey.ac.uk, mark.chambers1@apha.gov.uk (M.A. Chambers), graham.smith@apha.gov.uk (G.C. Smith), dez.delahay@apha.gov.uk (R.J. Delahay), r.mcdonald@exeter.ac.uk (R.A. McDonald), peter.brotherton@naturalengland.org.uk (P.N.M. Brotherton).
[1] Present address: Department of Environment, Food and Rural Affairs, Horizon House, Deanery Rd, Bristol BS1 5TL.

https://doi.org/10.1016/j.prevetmed.2025.106464
Received 13 May 2024; Received in revised form 10 February 2025; Accepted 11 February 2025
Available online 14 February 2025

of test-positive animals and restrictions on movement to limit further spread (Schiller et al., 2010). However, despite the application of such measures, there are several factors that make bTB a challenging disease to control. For example, diagnostic tests for cattle are imperfect, potentially missing a proportion of infected animals (Conlan et al., 2012), and any testing regime needs to balance maximising control benefits with limiting negative economic impacts on the livestock industry. *M. bovis* can also survive in a range of substrates (Scanlon and Quinn, 2000; Fine et al., 2011), creating opportunities for persistence in the environment and thus indirect transmission of infection. In several countries, wild mammal species may become infected with *M. bovis,* which can further complicate the control of the disease, particularly where these wild populations act as sources of infection to livestock (Palmer et al., 2012).

The European badger (*Meles meles*) is a wildlife host for *M. bovis* in several countries, including France, Spain, the United Kingdom and Ireland (Gortázar et al., 2012). In the UK and Ireland badgers are the principal wildlife host for *M. bovis* (Ní Bhuachalla et al., 2014; Godfray et al., 2018), with genetic evidence that infection can be sustained within badger populations, and transmitted from badgers to cattle, and from cattle to badgers (Biek et al., 2012; Crispell et al., 2019; Rossi et al., 2022). Studies of *M. bovis* prevalence in other wild mammals in England have found some degree of infection in almost all species surveyed, including rodents, small carnivores and deer (*Cervidae* spp.) (Delahay et al., 2007). Examination of the disease pathology in these species, along with other behavioural and ecological risk factors, suggests that most species act as spillover hosts, with little risk of onward transmission (Delahay et al., 2007). However, deer species, particularly social herding species (red deer *Cervus elaphus,* and fallow deer *Dama dama*), along with wild boar (*Sus scrofa*), have the potential to be sources of infection for cattle in some countries and ecological contexts (Ward et al., 2009; Foyle et al., 2010; Palmer et al., 2012). However, in the UK, the contribution of wild mammals other than badgers appears to be limited.

To date, actions to control *M. bovis* infection in badger populations have primarily consisted of culling, which aims to reduce the number of infected badgers in the landscape, and therefore the likelihood of onward transmission to cattle. In Ireland, research has shown that culling badgers is associated with reduced TB incidence in cattle (Griffin et al., 2005), and large-scale culling has been conducted in the country for several decades, focused on land surrounding cattle herd disease outbreaks (termed 'breakdowns'). In the UK, the use of badger culling varies amongst the different nations, with no recent large-scale culling in Wales or Northern Ireland and Scotland is Officially TB Free. In contrast, large-scale farmer-led badger culling began in England in 2013, supported by evidence from an earlier field trial (the Randomised Badger Culling Trial – RBCT, 1998–2005) that demonstrated culling badgers could reduce TB incidence in cattle if conducted proactively over large areas for multiple years (Donnelly et al., 2003, 2007; Jenkins et al., 2010). Recent analyses indicate that the policy of badger culling alongside cattle control measures in England has resulted in a significant reduction in TB incidence in cattle (Downs et al., 2019; Birch et al., 2024).

A non-lethal option for controlling disease in wild populations is via vaccination, either by parenteral delivery to trapped individuals or via the deployment of edible vaccine baits (Cross et al., 2007). Badgers were first identified as a host for *M. bovis* in England in 1971 and early reviews of disease control options considered the possibility of badger vaccination (Zuckerman, 1980). A review of TB control in England by Krebs (1997) recommended that research be undertaken to develop a vaccine for badgers. Following several years of research, an injectable BCG vaccine was licenced for use in 2010 (Brown et al., 2013). Current practice in the UK is for the vaccine to be administered to badgers caught in baited cage traps (Benton et al., 2020), although in Ireland trapping is supplemented by the use of wire restraints to live capture badgers for vaccination (Byrne et al., 2012b).

Since being licenced in 2010, more than 10,000 doses of the BadgerBCG vaccine have been delivered to badgers trapped in the UK (APHA, unpublished data). The precise number of badgers vaccinated is not known, as they are not routinely marked with a unique identifier and some badgers will have been vaccinated more than once. However, the scale of badger vaccination in the UK has been relatively small compared to culling programmes, with vaccination delivered by volunteer groups and non-government organisation, alongside a small number of government-delivered projects (Benton et al., 2020). For example, in England in 2020, 1094 badgers were vaccinated over an area of 283 km^2, compared to more than 40,000 badgers culled over an area of 27,708 km^2; so, whilst the intensity of vaccination has been greater than culling per unit area, the geographical range over which it has been conducted, has been far less. In the Republic of Ireland, badger vaccination has been a policy within the Irish bTB eradication programme since 2018, with many large areas transitioning from badger culling, and a future intention to use vaccination as a long term, sustainable option for reducing the infection risk posed to cattle by badgers (Ryan et al., 2023).

An independent review of the English government's TB control strategy conducted in 2018 stated that "moving from lethal to non-lethal control of the disease in badgers is highly desirable", due to public opposition to lethal control and its potential impacts on badger populations (Godfray et al., 2018). In its response, the Department for Environment, Food and Rural Affairs (Defra) stated an intention to transition from badger culling to large-scale vaccination as the primary form of TB control in badgers in the future (Defra, 2020). However, there are several challenges to expanding badger vaccination in England, including issues relating to training, logistics, funding and delivery. In addition, key stakeholder groups remain sceptical of the efficacy of badger vaccination, which can potentially limit uptake and deployment (Enticott et al., 2012). While there are many studies investigating aspects of badger vaccination (Robinson et al., 2012), there are significant gaps in the evidence base. This narrative review summarises the key evidence informing the use of badger vaccination as a tool for TB control, highlights the limitations and identifying areas for further research.

1.1. Captive studies of vaccine efficacy in badgers

Multiple experimental trials have been conducted on captive badgers to investigate the effect of vaccination against *M. bovis* infection (Table 1). The majority of studies involve the Bacillus Calmette-Guérin (BCG) vaccine, which is a live attenuated vaccine, used in humans since the 1920s where it has a variable reported efficacy of 0–80 %, with an average of 50 % (Brewer, 2000). Vaccine studies on captive badgers typically involve one or more experimental groups which receive the vaccine, delivered at different doses or via differing routes, which are then compared to a control group receiving no vaccine. The earliest such study by Stuart et al. (1988) consisted of a series of experimental trials, the first of which involved experimental infection with *M. bovis* of four badgers via intradermal injection, resulting in generalised infection and a measurable immune response. In a second experiment, 12 badgers were vaccinated with BCG intradermally, producing a LTT (Lymphocyte Transformation Test) response, consistent with cell mediated immunity. Seven of the vaccinated badgers were then subjected to intradermal challenge with *M. bovis*, and while the details in the study are quite sparse, the authors concluded that vaccinated badgers survived longer post infection and shed fewer *M. bovis* bacilli than un-vaccinated badgers.

Since the work by Stuart et al. (1988) there have been a further 17 published studies investigating the effects of BCG vaccination on badgers in a captive setting, with a range of vaccine doses administered via a variety of routes (Table 1). Most of these studies have involved challenge with *M. bovis*, but in some instances they have focused primarily on measuring immune responses to the vaccine (Table 1). For example, Southey et al. (2001) vaccinated badgers by subcutaneous injection with BCG Pasteur and compared their immune responses to those of animals

Table 1
Summary of experimental vaccination trials on captive badgers.

Reference	Route*	Treatment groups	BCG strain	vaccine dose (CFU)	Challenge	Responses measured	Results
Stuart et al. (1988)	ID	Vaccinated (n = 12), Control (n = 4)	Not stated	Not stated	Y	Immune response (lymphocyte transformation tests, ELISAs, skin test). Bacterial shedding, Clinical examination of injection site. Badger survival time.	Vaccinated badgers lived longer, shed fewer bacilli and inoculation sites healed more rapidly
Southey et al. (2001)	SC	Vaccinated (n = 9 at week 0, 18 and 30), Control (n = 6)	Pasteur	5×10^4 (week 0 and week 18), 5×10^5 (at week 30)	N	Comparative lymphocyte transformation assay (LTA) to measure cell mediated response	Enhanced response to PPD-bovine detected in vaccinated group, but only following three vaccine doses
Lesellier et al. (2006)	SC, IM	Vaccinated SC (n = 3), Vaccinated IM (n = 3), Control (n = 2).	Danish	'Overdose' of 5–22 $\times 10^7$ and follow-up dose of 4–7 $\times 10^5$	N	Clinical examination of injection site, blood sampled for haematology and immunology, weight and behaviour changes.	Mild reactions at injection site, particularly for intramuscular route. No change in behaviour, body weight or temperature. Increased cellular immune response in vaccinated animals within 13 days of vaccination and maintained for 76–105 days post. No evidence of BCG shedding.
Corner et al. (2008)	SC, M	Vaccinated SC (n = 4), Vaccinated M (n = 5), Control (n = 5).	Pasteur	SC (5 $\times 10^5$), M (4 $\times 10^4$)	Y	Gross pathology, histopathology and bacteriology	Vaccinated group had significantly fewer and less severe lesions, fewer sites with histological lesions
Lesellier et al. (2009)						Immunological responses, change in IFN-y expression and response to several key antigens	Protective immune response in vaccine group. Vaccinated badgers had a response earlier post infection to PPD-B than unvaccinated badgers. Release of IFN-y in control badgers later and much higher than vaccinated badgers
Corner et al. (2010)	O	Vaccinated (n = 7), Control (n = 7)	Danish	10^8 CFU	Y	Gross pathology, histopathology, bacteriology and immunology.	Vaccine group had fewer sites with gross lesions, decreased severity of gross lesions, fewer infection sites, and lower bacterial load compared with the control group
Chambers et al. (2011)	IM	study 1: Vaccinated (n = 3), Control (n = 2), study 2: Vaccinated (n = 6), Control (n = 4)	Danish	5.4×10^6 3.2×10^6	Y	Gross pathology, histopathology, bacteriology and immunology.	Vaccinated badgers had lower lesion scores, a lower culture positive rate and took longer to yield positive results compared to controls
Lesellier et al. (2011)		study 2* : Vaccinated - high dose (n = 6), Vaccinated - low dose, Control (n = 4)		3.2×10^6 (high) 3.3 x 10^5 (low)		Gross pathology, histopathology, bacteriology and immunology.	High dose group had lower disease severity score and fewer sites containing AFB than control. No differences between low dose and control. Vaccinated groups had lower excretion rates than control group. Vaccinated badgers positive to PPD-B (IFNy)
Murphy et al. (2014)	O	Vaccinated - BCG Danish (n = 7), Vaccinated - BCG Pasteur (n = 6), Control (n = 8)	Danish / Pasteur	108	Y	Gross pathology, histopathology, bacteriology and immunology.	Vaccinated badgers had less gross pathology, lower gross pathology severity scores, fewer sites with histopathological lesions, fewer sites of infection and lower bacterial loads in tissue than control badgers.
Chambers et al. (2017)	O	Study 1: BCG - oral delivery (n = 4), BCG - high dose oral lipid (n = 8), control (n = 8) Study 2: BCG - high dose oral lipid (n = 4), low dose oral lipid (n = 7), control (n = 8)	Danish Danish	9×10^7 (oral delivery) 2–3 $\times 10^8$ (high dose lipid), 10^7 (low dose low dose lipid)	Y	Bacteriology/culture clinical samples, IFNy and Elispot and antigens, histopathology	Study 1 - Evidence of protection in vaccinated groups (fewer lesions, histopathology), Study 2 - Evidence of protection in low dose group (fewer lesions, histopathology, but not high dose group

(*continued on next page*)

Table 1 (*continued*)

Reference	Route*	Treatment groups	BCG strain	vaccine dose (CFU)	Challenge	Responses measured	Results
Perret et al. (2018)	O	Three vaccinated groups (each containing three vaccinated badgers and one unvaccinated 'sentinel') and one control group (containing four un-vaccinated badgers)	Danish	8×10^9 followed by 6–7 $\times 10^7$	N	Clinical examination, culture of faecal samples, followed by postmortem analysis of all animals at end of study	No evidence of change in clinical signs, BCG cultured from three faecal samples within 48hrs of vaccination. No BCG or AFB identified in tissues at post-mortem.
Lesellier et al. (2019)	O, Enteric (capsule)	Study 1: Vaccinated - intellicap capsule (n = 6), Vaccinated -manual delivery (n = 6),	Danish	5.67×10^7	N	Immunology, histopathology, *post-mortem* examination with culture and PCR of tissues/ lymph nodes	BCG culture in tissues at end of study (8 weeks post vaccination). Mild pathological features and induced the circulation of IFNγ-producing mononuclear cells. Vaccination resulted in reliable uptake by associated lymph nodes in manual oropharyngeal delivery, but not enteric capsule delivery.
	O	Study 2: Vaccinated - BCG + peanut oil (n = 4), Vaccinated - BCG + coca butter		6.73×10^7			
Balseiro et al. (2020)	O	Vaccinated with BCG (n = 5), Vaccinated with heat-inactivated *M. bovis* (HIMB) (n = 7), Control (n = 12)	Danish/ Heat-inactivated *M. bovis* (HIMB)	10^8 (BCG), 10^7 (HIMB)	Y	Immunology (IGRA, IFN-γ), *post mortem* examination, MRI, bacteriology and PCR of tissues sampled, Histopathology	Number of badgers positive to elisa higher in control than vaccine groups. Lower lesion score in vaccine groups, no difference between vaccines. Lower bacterial burden in vaccinate groups. Promising results for HIMB.
Blanco Vazquez et al. (2020)						Immunohistochemistry - quantifying cells within TB granulomas. Image analysis of lung tissues.	Higher proportion of macrophages in BCG group than control. Lower bacterial load and smaller lesion areas in vaccinated groups than control
Lesellier et al. (2020)	O	Study 1: Vaccinated high dose (n = 10), Vaccinated low dose (n = 20), Control (n = 10).	Danish	1.2×10^9 (high dose), 2.0×10^8 (low dose)	Y	Gross pathology, histopathology, bacteriology and immunology. Calculated disease burden score.	Lower disease burden score in manually vaccinated badgers than control (in both studies) – no difference between high dose and low dose. No evidence of protection from vaccine baits.
		Study 2: Vaccinated (n = 8), Vaccinated (BCG in baits, n = 20), Control (n = 10)	Danish	$8.4–8.6 \times 10^8$			
Juste et al. (2023)	O	Vaccinated with heat-inactivated *M. bovis* (HIMB) (n = 8), Control (n = 7)	Heat-inactivated *M. bovis* (HIMB)	Five baits containing 10^7 (with a second batch approx. 60 days later)	Y	Gross pathology, histopathology, bacteriology, immunology (IGRA, IFN-γ,P22), MRI of lung tissues. Calculated disease burden score.	HIMB vaccinated animals had higher disease scores than controls, partly due to two divergent vaccinates with very high values. Six non-divergent vaccinates had lower bacterial load and pathology than controls.

* ID=Intradermal, SC=Subcutaneous, M=Mucosal(intranasal/conjunctival), IM=Intramuscular, O=Oral

in an unvaccinated control group. Vaccinated badgers exhibited a T-lymphocyte response to the antigen PPD–B (bovine purified protein derivative of *M. bovis*), a measure of cell-mediated immune response against *M. bovis*, although this difference was only significant after three doses of the vaccine (Southey et al., 2001).

With the exception of Stuart et al. (1988), all challenge studies have involved *M. bovis* delivery via the endobronchial route directly into the airway, as this has been shown to generate consistent infection, with pathology similar to that observed in naturally infected badgers (Corner et al., 2007). Challenge studies typically assess infection in several ways, including microbiological culture of samples, evidence of gross disease following *post-mortem* examination, and histopathology, along with a suite of tests to measure immune responses in vaccinated and control animals (Table 1). For example, Corner et al. (2008) demonstrated that subcutaneous BCG vaccination led to decreased severity of disease and reduced dissemination of infection, with fewer sites with gross lesions and less severe lesions than control animals. Further analysis of samples from this study by Lesellier et al. (2009) showed that BCG vaccination led to a protective immune response, as evidenced by a more rapid response post-infection to bovine PPD stimulation, and a lower and earlier release of IFN-γ in vaccinated badgers compared to controls.

Although BCG delivered via a variety of routes has provided evidence for protection against infection with *M. bovis* in badgers (Table 1), the only currently licenced method for field delivery is by intramuscular injection (Brown et al., 2013). Trials on captive badgers have shown that intramuscular injection of BCG is safe, with mild inflammatory reactions at the injection site, no effects on body weight or behaviour, and no excretion of BCG, even following a large overdose of the vaccine (Lesellier et al., 2006). Two subsequent experiments investigated protection following intramuscular administration of BCG. The first involved three badgers vaccinated with a dose of 5.4×10^6 CFU and two unvaccinated control badgers (Chambers et al., 2011) while the second involved six badgers vaccinated with a similar high dose of 3.2 x 10^6 CFU, eight with a lower dose of 3.3 x 10^5 CFU, and four unvaccinated controls (Lesellier et al., 2011). The low dose is equivalent to the adult human dose of BCG (one tenth of a vial), with the high dose consisting of an entire vial of BCG, or ten human doses. Badgers vaccinated with the higher doses of BCG vaccine had significantly lower lesion scores

compared to unvaccinated badgers, and *M. bovis* was cultured in a smaller proportion of individuals and at a later stage in the experiment, compared to unvaccinated badgers (Chambers et al., 2011). Further histological analyses by Lesellier et al. (2011) demonstrated that fewer badgers in the higher dose vaccine group had tissues containing evidence of acid-fast bacteria (a further measure of *M. bovis* infection) compared to both the control and low dose groups. While there was some evidence of vaccine efficacy in the low vaccine dose group, with lower disease severity scores than for unvaccinated badgers, greater levels of protection were evident for the higher vaccine doses (Lesellier et al., 2011). For example, while 7/8 badgers receiving the lower vaccine dose shed *M. bovis* during the experiment (positive culture samples), only 3/9 badgers in the higher dose group did so (Lesellier et al., 2011). This evidence of reduced disease progression, severity and *M. bovis* excretion associated with the higher dose treatments informed the licencing of the injectable BadgerBCG vaccine in 2010 in the UK, which consists of BCG Danish at a dose of 2–8 $\times$ 10^6 CFU (Brown et al., 2013). While BCG Danish 1331 is the most widely used strain in badgers, BCG Sofia SL2222 has also been used in some badger vaccination projects, primarily due to issues with vaccine supply (Benton et al., 2020; Courcier et al., 2022)

Whilst intramuscular injection is the only currently licenced route for BCG vaccine delivery in badgers, most captive experimental studies have involved oral delivery of BCG (Table 1). Oral vaccination is generally viewed as a more efficient approach for free-living wildlife, as the vaccine can be contained in edible baits and deployed in the environment, requiring no capture or handling of animals (Cross et al., 2007). Oral vaccines have been used to successfully control a limited number of other diseases in wildlife, such as rabies and classical swine fever (von Rüden et al., 2008; Mähl et al., 2014), and the merits and challenges for the delivery of an oral TB vaccine to badgers have been described (Delahay et al., 2003). Multiple experimental studies have shown that orally administered BCG has a protective effect against *M. bovis* reducing the number and severity of lesions, along with other measures of disease (Corner et al., 2010; Murphy et al., 2014). However, immunity afforded by orally administered BCG has also been shown to be inconsistent. Chambers et al. (2017) conducted two experiments to investigate the protective effects of orally administered BCG in solution, or within a lipid matrix at two doses (Table 1). In the first study, post-mortem examination of badgers that had received the higher dose lipid-based vaccine had evidence of protection, with lower TB lesion scores and fewer sites with histological lesions than unvaccinated controls. However, in the second study the same high-dose lipid vaccine resulted in no significant differences in TB lesion prevalence or scores relative to control animals, but there were significant reductions in the lower dose vaccine group. More recent challenge experiments using a similar high dose of the vaccine administered directly into the oral cavity demonstrated evidence of protection against infection and disease associated with *M. bovis*, with lower disease burden scores in vaccinated groups compared to controls (Lesellier et al., 2020). However, there was no evidence of protection in badgers when the same vaccine dose was contained in edible lipid baits (Lesellier et al., 2020).

It is not known what the critical site or sites, are for immune induction following oral administration of BCG, although it is believed that the oral cavity is important and that uptake directly into the ileum is less likely to produce a protective effect (Lesellier et al., 2019). The high variation in protection observed amongst oral vaccine studies (Chambers et al., 2017), particularly those involving edible baits (Lesellier et al., 2020), may relate to variable absorption of the vaccine in the oral cavity.

Recent experimental challenge studies using heat-inactivated *M. bovis* have also been encouraging (Balseiro et al., 2020; Blanco Vázquez et al., 2020; Juste et al., 2023) and may suggest a viable alternative to the use of live BCG, which has a short shelf-life and requires refrigeration until use. However, it seems unlikely that there will be a licenced oral badger vaccine for badgers available in the short to medium term, with the injectable BCG vaccine the only option available currently.

1.2. Field studies of vaccine efficacy in badgers

Field trials can involve comparisons amongst groups of individuals receiving different vaccine doses or levels of coverage (% vaccinated). Field studies have the advantage that it may be possible to test and evaluate effects of the vaccine in a large number of individuals, against naturally acquired infection, in a population subject to a natural level of disease exposure. However, the lack of control over field studies means that levels of pathogen exposure and epidemiological outcomes in individuals may be more difficult to quantify. In some cases, field studies may run in parallel to vaccine deployment projects, where the principal aim is to evaluate the project's outcomes (such as vaccine coverage), rather than to trial or compare differing experimental treatments, or quantify vaccine efficacy *per se*. Nevertheless, such real-world deployments of wildlife vaccines can produce valuable data which can be used post-hoc to estimate aspects of vaccine performance (von Rüden et al., 2008; Menzies et al., 2021).

To date there have been two large field trials investigating the protective effects of the BCG vaccine in free-living badgers (Table 2); the Badger Vaccine Study (BVS) in Gloucestershire, England (APHA, 2010; Chambers et al., 2011; Carter et al., 2012) and the Kilkenny vaccine trial in the Republic of Ireland (Aznar et al., 2011; Gormley et al., 2021). The two studies differed significantly in their size, methods, badger population and purpose. For example, the BVS took place over a 55 km^2 area, with 60 % of the resident badger social groups being randomly allocated to the vaccine treatment (vaccination by intramuscular injection) with the remainder serving as unvaccinated controls, with the primary aim of obtaining safety data for BCG licencing purposes. In contrast, the Kilkenny trial aimed to investigate how the reproductive ratio R (the number of new infections caused by each infected individual) varied with differing levels of vaccine coverage, with vaccination administered orally to badgers across a 750 km^2 area divided into three treatment zones (Aznar et al., 2011). However, despite these differences, both studies demonstrated consistent protective effects of BCG under field conditions.

Table 2
Details of the two field trials investigating vaccine efficacy in wild badgers.

	Badger Vaccine Study (BVS)	Kilkenny vaccination trial
Location	Gloucestershire, England	Kilkenny, Republic of Ireland
Area size	55 km^2	750 km^2
Period	2006–2009	2009–2013
Trapping frequency	Twice per year (cage trapped)	Twice per year (cage trapped and stop restraints)
Badger capture density	2.45 – 5.65 badgers per km^2 per capture event	0.16 – 0.40 badgers per km^2 * per capture event
Badger Population density	Not estimated	Overall density approx. 1.1 badgers per km2. Density within the study area varied from < 0.5 to > 10 badgers per km2*
Experimental treatments	60 % social groups vaccinated, 40 % unvaccinated controls	Three zones; A)100 % placebo; B)50 % vaccinated, 50 % placebo; C)100 % vaccinated
Vaccine	BCG Danish strain 1331 (2–8 $\times 10^6$ CFU) intramuscular injection. One dose per year captured.	BCG Danish strain 1331 (1 $\times 10^8$ CFU) in lipid medium, delivered orally directly onto the upper pharyngeal mucosa. One dose per year captured.
Measures of vaccine efficacy	*M. bovis* culture, IFNy immunoassay and Stat-Pak antibody test	Stat-Pak antibody test, Enfer multiplex antibody test and *post-mortem* examination of euthanised badgers

* (Byrne et al., 2024)

In the BVS, test negative badgers that were vaccinated were 74 % less likely to become test positive by the Stat-Pak antibody test at future trapping events compared to unvaccinated badgers and were 61 % less likely to test positive to either Stat-Pak or culture (Chambers et al., 2011). Further analyses by Carter et al. (2012), using a slightly different statistical approach, confirmed these results, with vaccinated badgers 76 % less likely to test positive to the double test (either Stat-Pak or culture) and 54 % less likely to test positive to a triple test of culture, Stat-Pak and IFNy, compared to unvaccinated badgers. Importantly, Carter et al. (2012) also demonstrated that vaccinating one third or more (>0.33) of adult badgers in a social group reduced the likelihood that unvaccinated badger cubs in that group would test positive by 79 % (CI 19 % - 95 %), thus demonstrating herd immunity at the social group level. However, there was no evidence of a benefit to unvaccinated adult badgers associated with the vaccination of other badgers in their social group.

In the Kilkenny trial, rates of seroconversion using the Stat-Pak test (transition from test negative to test positive) were significantly lower in vaccinated than in unvaccinated badgers, with a 36 % reduction for badgers enrolled in the early part of the study (trapping events 1–2 of 6) and an 84 % reduction in the later stages of the study (trapping events 3–6 of the 6) (Gormley et al., 2017). Vaccinated badgers that seroconverted were also test-negative for longer, compared to unvaccinated badgers (Gormley et al., 2017). Further analysis of data using results of the Enfer antibody test combined with data on vaccine coverage and TB prevalence, were used to quantify different transmission parameters and estimate the effect of vaccination on susceptibility to infection and infectivity (i.e. onward transmission from vaccinated badgers that were infected) (Aznar et al., 2011, 2018). Vaccination significantly reduced the likelihood that badgers would become infected with *M. bovis* by 59 %. However, there was no effect of vaccination on infectivity in the analyses, suggesting that although vaccination reduced the number of new infections, vaccinated badgers that became infected were still capable of transmitting *M. bovis* (Aznar et al., 2018). While vaccination did not appear to reduce infectivity, a reduction in the number of badgers susceptible to infection could still reduce *R0,* leading to disease control benefits. By combining estimates of vaccine efficacy (to susceptibility, 59 %) with data on TB prevalence in Irish badgers, Aznar et al. (2018) estimated that *R0* would decline to < 1, leading to a decline in the number of infected badgers if vaccine coverage was above 30 %. Mean trappability was estimated to be 34–35 % per session across the population. By the fifth capture session, 79 % of the adult badgers caught had been marked previously (Byrne et al., 2012a).

Further evidence of the impact of vaccination on TB prevalence in the Kilkenny trial was derived from the *post-mortem* examination of enrolled badgers (n = 173, test negative at first capture) that were euthanised at the end of the trial (Gormley et al., 2017, 2021). TB prevalence was significantly lower in badgers from the vaccination area where all trapped animals had been given the vaccine (24 % with confirmed infection), compared to the area where badgers were given a placebo (52 % with confirmed infection). A further 83 badgers caught for the first time at the final trapping event were also euthanised at the end of the study. Whilst TB prevalence in these previously unvaccinated badgers was comparable to that in the unvaccinated animals from zones A (100 % placebo) and B (50:50 vaccine:placebo), there was no evidence of infection (0 % prevalence) in any of those newly caught in zone C (100 % vaccinated) (Gormley et al., 2021).

The safety of badger vaccination has been investigated in captive conditions (Lesellier et al., 2006) with data also being collected in the field during the English BVS study. Data from the BVS indicated that BCG was not excreted by badgers vaccinated by intramuscular injection, and there was no evidence of adverse reactions to the vaccine (APHA, 2010). Research on the movement of vaccinated badgers using GPS collars also demonstrated that there was no detectable effect of vaccination on home range size, nightly distance travelled, or the probability of trespassing into neighbouring territories (Woodroffe et al., 2017). There was also no impact of the vaccination trapping operations on nightly ranging behaviour, suggesting that vaccination does not lead to the kind of changes in ranging behaviour that have been observed in culled populations (Carter et al., 2007). As vaccination does not lead to changes in behaviour, adverse physical reactions to the vaccine, or excretion of BCG, this indicates that vaccination will not have negative impacts on disease transmission or badger welfare.

Vaccination has also been deployed in combination with culling, in 'Test Vaccinate Remove' (TVR) approaches, where badgers are tested for TB, and test positive animals removed while test negative animals are vaccinated. A large-scale trial of TVR Northern Ireland over a 100 km^2 area resulted in a significant reduction in badger TB prevalence, falling from 14 % in year one to 1.9 % by the end of the five-year study. Relatively small numbers of test positive badgers were removed annually, equivalent to 16 %-6 % of badgers captured (Menzies et al., 2021). AS with vaccination there, was no evidence that TVR resulted in significant changes in home range sizes or ranging behaviour of badgers remaining in the population, with the exception of short term increase in ranging behaviour in the eight nights after capture (Redpath et al., 2023).

1.3. Lessons from badger vaccination field deployment in England and Wales

Since it was licenced in 2010, the injectable BadgerBCG vaccine has been administered to wild badgers as part of several badger vaccination projects in England, Wales and Ireland. Unlike the BVS and Kilkenny trial, these projects represent operational deployment and were not designed as research studies, but they do offer opportunities to collect valuable data relating to badger vaccination. For example, the Badger Vaccine Deployment Project (BVDP) was a UK Government delivered project conducted from 2010 to 2014 in Gloucestershire, with up to 1000 badgers vaccinated annually over a 100 km^2 area, and the broad aim of providing information on the logistics of large scale badger vaccination (APHA, 2015). Analysis of data from the BVDP and several smaller vaccination projects indicated that trapping efficiency (the percentage of set traps resulting in capture) varied seasonally, peaking in July, but was similar for Government and volunteer led initiatives (Benton et al., 2020). Trapping data from these projects was also analysed to estimate the percentage of badgers vaccinated annually, which had an average of 57 % (95 %CI 48–63 %) across all areas (Benton et al., 2020). This estimate closely matches that of Smith et al. (2020), who compared the genotypes of badgers collected from remote hair traps to those from cage-trapped vaccinated individuals in a 288 km^2 area in Pembrokeshire, Wales termed the Intensive Action Area or IAA.

In the IAA, badger vaccination was conducted from 2012 to 2015, as part of a programme of intensified cattle controls, enhanced TB testing and heightened biosecurity initiated in 2010. This study estimated that 40–60 % of badgers in the IAA were vaccinated annually, equating to a cumulative 67–83 % of the population having received at least one dose of vaccine by the end of the four-year project. Road-killed badgers were also collected from within the IAA for *post-mortem* examination. In year one, 19 % (95 % CI 8–35 %) of carcasses recovered had evidence of *M. bovis* infection compared to only 4 % (95 % CI 0.1–20.4 %) in year four of the study (APHA, 2016a). While the level of uncertainty for these estimates is large due to the small number of badgers analysed (n = 25–37 per year), the trend is consistent with declining TB prevalence in badgers over time.

More recently, (Woodroffe et al., 2024) used a combination of camera traps and blood sampling to evaluate to evaluate a small scale (11 km^2) badger vaccination programme in Cornwall, England. Vaccination coverage was estimated at 74 % and was associated with significant changes in TB prevalence in badgers, declining from 16 % (95 % CI 4.5 %–36.1 %) in year one, to an apparent prevalence of 0 % (95 % CI 0 %–8.8 %) by the end of the four-year study.

Increased uptake of badger vaccination in England will include areas

transitioning from several years of culling, whereas previous vaccination programmes have usually taken place in high density undisturbed badger populations. Trapping for vaccination in post-cull areas presents challenges related to the reduced density and disrupted spatial organisation of resident badger populations. However, analysis of trapping data indicated that capture rates from the BVDP were broadly consistent with those from a vaccination project carried out on recently culled land in Cumbria (Benton et al., 2023). But workshops with the highly experienced trappers who carried out operations in Cumbria indicated that they had adapted practices to take account of the challenges of trapping badgers in previously culled areas. For example, they recognised that field signs may be scarcer and hence more difficult to interpret, badgers may be more neophobic and slower to become accustomed to the bait used to lure them into traps (Benton et al., 2023).

1.4. Modelling the effects of badger vaccination on TB in badgers and cattle

Mathematical and simulation models have a long history of use in TB research. Early modelling studies of TB in badgers focused primarily on understanding disease dynamics in infected badger populations (Anderson and Trewhella, 1985; Bentil and Murray, 1993; Smith et al., 1995; White and Harris, 1995b), with later studies investigating the relative performance of different control strategies, including badger vaccination (White and Harris, 1995a; Smith and Cheeseman, 2002; Wilkinson et al., 2004). To date, most studies investigating the impacts of badger vaccination have utilised an individual-based, spatial, stochastic, simulation model, initially developed by Smith and colleagues (Smith et al., 2001; Wilkinson et al., 2004) and later modified to reflect contemporary data on vaccine efficacy to evaluate the impacts of different control strategies on both badgers and cattle (Smith and Delahay, 2018). This model has been used for research purposes and also to directly inform field operations, including the IAA project in Wales (Smith and Budgey, 2016) and a TVR trial in Northern Ireland (Smith et al., 2013). However, other alternative modelling approaches have also been employed to investigate the effectiveness of badger vaccination (Hardstaff et al., 2013; Abdou et al., 2016).

Modelling studies consistently predict that badger vaccination will lead to declines in the level of infection in badger populations (White and Harris, 1995a; Smith and Cheeseman, 2002; Smith et al., 2012), although the rate and magnitude of its impact may depend on factors such as badger density and vaccine coverage (Wilkinson et al., 2004; Hardstaff et al., 2013). Wilkinson et al. (2004) compared reactive badger vaccination (i.e. in localised areas following cattle TB outbreaks) to a proactive strategy (i.e. broad scale and independent of infection in cattle) with varying badger density and vaccination coverage. Small scale reactive approaches were less effective than large scale strategies. For example, 10 % vaccine coverage in 80 % of badger social groups was more effective than 80 % coverage in only 10 % of groups. The elimination of TB from the badger population was possible where vaccine coverage was 30–40 %, which is similar to a later estimate based on field data in Ireland (Aznar et al., 2018). However, eradication of TB in badgers was predicted to take 20–30 years of annual vaccination, even when coverage was $>$ 70 % (Wilkinson et al., 2004). Hardstaff et al. (2013) predicted that vaccination could eliminate TB from badger populations or at least reduce prevalence to $<$ 1 %, in up to 10 years. Although such rapid reductions were only possible at badger group sizes of 4–6 individuals and with no external source of infection. Reductions in TB prevalence were achieved across a range of badger density scenarios and with vaccine efficacy set at either 50 or 80 %, but benefits were lower at higher densities (8–12 badgers per group) and where models included external sources of infection (Hardstaff et al., 2013).

Comparisons between the outcomes of different simulated strategies to control TB in badgers generally predict that vaccination will be less effective than culling when applied to high density badger populations (Smith et al., 2012; Abdou et al., 2016), which is in agreement with generic disease control models comparing culling and vaccination of wildlife (Barlow, 1996; Smith and Cheeseman, 2002). For example, Smith et al. (2012) compared different management strategies across a 150 km^2 control area and surrounding 2 km buffer, including badger vaccination, badger culling in isolation and in combination with ring vaccination (in the buffer). These models assume conditions broadly similar to large scale badger control operations in England, with 70 % of farms participating for five years, trapping of 70 % of badgers annually across a high density (7.5 badgers per group) population with high TB prevalence (17 %). Under these conditions, vaccination is still predicted to reduce TB in both badgers and cattle, although benefits are lower than for culling. For example, over the core and buffer area with control implemented in the first five years of a ten-year period, vaccination was predicted to reduce the rate of cattle herd breakdowns by 11 %, compared to 18 % for culling. Although badger vaccination had a lower impact on the number of infected badgers compared to culling, it resulted in a gradual consistent reduction in TB prevalence in both the core and buffer area, whilst culling caused a fall in total population size but an increase in prevalence in both areas during the period of control, resulting in a short term increase in cattle herd breakdowns (CHB) in the 2 km buffer (Smith et al., 2012). These negative impacts of culling were offset by vaccinating in the surrounding area, with the culling plus ring vaccination strategy resulting in the greatest reduction (-28 %) in CHBs over ten years. Models of TVR, involving the removal of test positive badgers and vaccination of test negatives, also suggest that a combined approach could be more effective than either non-selective vaccination or non-selective culling alone, however only in situations where TVR does not result in social perturbation of the badger population (Smith et al., 2016).

More recently, Smith and Budgey (2021) modified their earlier model to evaluate a range of potential future TB control options in England and how these might impact badger population size and levels of infection. The model assumes four years of initial badger culling, followed by one of several candidate approaches which would continue indefinitely; no control; further culling; badger vaccination; vaccination combined with fertility control; along with multiple less regular culling strategies (biannual, triannual etc). The results suggested that culling would cause an initial steep decline in the number of infected badgers, but that all control strategies (including vaccination) resulted in a similar subsequent slow decline in the number of infected badgers over time, although there were different predicted outcomes regarding total badger population size. While culling strategies maintained the badger population at a low level, vaccination resulted in a gradual return to pre-cull levels, taking approximately 13 years, unless it was combined with fertility control, which is not available (Smith and Budgey, 2021).

Although most modelling studies evaluating badger vaccination have focused on England, some models have investigated different management strategies in Northern Ireland (NI) (Smith et al., 2013, 2016) and the Republic of Ireland (Abdou et al., 2016; Chang et al., 2023). While Smith et al. (2016) found broadly similar relative outcomes for the modelled vaccination strategies when comparing NI and England, the predicted outcomes of vaccination in ROI are significantly different from English models (Abdou et al., 2016). For example, using data based on Irish badger populations, Abdou et al. (2016) predicted that culling eliminated TB (100 % decline) from the badger population after 10–12 years, although not without risking extinction. In contrast, TVR or vaccination for 20 years only reduced TB prevalence by 70 % and 17 % respectively. The relatively poor performance of vaccination in this model may be due to differences in the underpinning parameters. For example, in the Irish model badger group size was 5.3, 45 % of the starting badger population was infected, trapping efficiency was 47 % and vaccine efficacy was 50 % (Abdou et al., 2016), which compares to values of 7.5, 17 %, 70 % and 70 % respectively in Smith et al. (2012) models of England's epidemiology.

Date collected from the Irish Kilkenny trial have also been used to model the impact of badger vaccination and other control options using

a spatially explicit multi-host model which includes transmission routes within/between herds and species (Chang et al., 2023, 2025). The results suggest that badger vaccination can have disease control benefits reducing the overall between-herd R rate from 1.21 to 0.85 (Chang et al., 2023). However, despite this regional benefit, 30 % of herds within the area were still estimated to have an R value > 1, potentially acting as sources of infection. These models suggest that the benefits of badger vaccination may depend on badger density, and an expansion of this modelling approach has been used to evaluate other measures such as badger culling, biosecurity and cattle vaccination (Chang et al., 2025). How vaccination efficacy is incorporated into models also likely influences model predictions. In most studies, badgers move between several disease states, typically susceptible, infected and/or infectious, with vaccination providing complete lifelong immunity to susceptible individuals with a certain probability (vaccine efficacy) and no protection to others. To test the robustness of these assumptions, Smith et al. (2022) compared several scenarios where the probability of vaccinated susceptible badgers receiving full protection varied from 60 % to 90 %, with the remaining animals receiving either no protection, or varying levels of partial protection against becoming either infected or infectious. Including partial protection in the model generally increased the impact of badger vaccination on TB prevalence, although this was not the case in models where individuals receiving partial protection from their first vaccination event were prevented from gaining full protection in the future. However, generally the outcomes for most plausible scenarios were similar to default values used in earlier vaccination models assuming a fully protective BCG vaccine (e.g., Smith et al., 2012).

There have been no published comparisons of vaccination modelling studies and field trials for TB in badgers, however work has been presented that compared the NI TVR study with a model outcome that had a high level of agreement on the decline in prevalence in badgers during the study (Smith unpublished data).

1.5. Field evidence for the effect of badger vaccination on TB in cattle

To date the only field trial conducted specifically to investigate the impacts of badger vaccination on TB in cattle took place in seven counties in the Republic of Ireland from 2011 to 2017 (Martin et al., 2020). This was a non-inferiority study aimed at determining whether badger vaccination was any less effective than targeted badger culling (the primary method of disease control at the time) at controlling bTB. Badger vaccination was conducted over large contiguous areas of 250–500 km^2 in each county, equivalent to 8–38 % of the county area, with targeted badger culling continuing on the remaining land. Badger culling had taken place for several years in each county prior to the vaccination and culling treatments being applied. As with studies investigating the impacts of badger culling on cattle (Griffin et al., 2005; Donnelly et al., 2007), the primary outcome of interest was new TB herd incidents in cattle, which in this study were new TB breakdowns with > 2 skin test reactor cattle (Martin et al., 2020). A "small acceptable risk difference" was set at 1 %, such that badger vaccination would be deemed inferior if vaccinated areas had a 1 % higher incidence rate in cattle relative to cull areas. Analyses controlling for factors relevant to bTB risk (herd type, herd size, prior TB history) found no difference in bTB incidence rates between vaccinated and culled areas in four counties, suggesting vaccination was not inferior to culling (Martin et al., 2020). However, in the other three counties (County Cork North, Galway and Monaghan), TB incidence was significantly higher in vaccinated areas compared to culled areas. In County Cork North, the increase in incidence began prior to the start of vaccination and then declined during the later years of the trial, suggesting that vaccination was not the cause, but its impact was deemed 'ambivalent'. In counties Galway and Monaghan, vaccination was deemed inferior to culling, although higher TB incidence in Galway was linked to cattle purchasing behaviour. As a larger proportion of herds in the Galway vaccinated area (87 % of vaccinated herds, compared to only 3.4 % herds in culled area) purchased from a mart sourcing cattle from areas of higher TB risk. Overall badger densities were estimated to be 40 % higher in vaccinated compared to culled areas during the trial, although in County Monaghan there was no evidence of a significant rise in badger number within the vaccinated area, suggesting that a lack of population control was not a likely cause of rising TB in cattle. Martin et al. (2020) therefore concluded that vaccination was not-inferior to culling in five of the seven counties tested, and that their study had demonstrated that a transition from culling to vaccination could form part of the BTB-Eradication-Program in the ROI, and subsequently the Irish Government proceeded with wider deployment of badger vaccination nationally (DAFM, 2021).

No trials have been conducted with the aim of investigating the impacts of badger vaccination on bTB incidence in the UK, although trends have been quantified in two areas where badger vaccination took place and show a concomitant reduction in TB incidence (APHA, 2016c, b). In the Intensive Action Area (IAA) in Wales. From 2010–2016, TB incidence in the IAA fell by 35 % compared to only 23 % for the comparison area, accompanied by reductions in the proportion of herds under TB restrictions (APHA, 2016c).However, the implementation of multiple disease control measures in cattle prior to and alongside badger vaccination means their relative contributions could not be determined. The comparison area chosen in the report also differed from the IAA in several important respects (e.g. size, TB history and cattle population) and the analyses conducted were purely descriptive, outlining broad trends, with no attempt to control for these covariates or estimate a treatment effect or difference between the areas. As a consequence, authors of the APHA (2016c) report, are cautious in their interpretation, highlighting that the IAA and comparison area were not directly comparable and that differences in TB in cattle between the two areas could relate to differences in surveillance and control strategies.

The second large scale vaccination project which presents opportunities to investigate impacts of badger vaccination on bTB was the BVDP in Gloucestershire, England. This was a five-year project designed to collect information on the practicalities of badger vaccination and provide training opportunities for lay vaccinators (APHA, 2015). As with the IAA, the study did not aim to investigate the impacts of badger vaccination on cattle, although descriptive analyses of bTB trends were conducted after the project was completed (APHA, 2016b). The main analysis looked at cattle herd TB incidence in the BVDP and four comparison areas of similar TB history, herd size, herd number and historical badger culling. The bTB incidence rate fell significantly in the BVDP over the five years the project was implemented (2010–2014), with a particularly steep drop in the final year (APHA, 2016b). However, significant reductions in bTB incidence were also apparent in three comparison areas over the same period. While the authors state that the decline in both the BVDP and comparison areas may indicate that vaccination did not affect bTB incidence, they also highlight several important limitations of this work, concluding that it was difficult to draw any firm conclusions regarding the impact of badger vaccination on bTB incidence. Analyses of the BVDP data are limited by the sample size (one single 100 km^2 area), the focus on simple univariate trends (TB incidence vs time) and no attempt to control for other factors which may influence TB incidence in cattle, such as herd type and size. As with the IAA report, there were also no attempts to estimate a treatment effect or difference between the BVDP and comparison areas, instead the trends in vaccination and comparison areas were simply quantified and then discussed. The importance of controlling for other factors is evident from analyses to evaluate badger culling in England. For example, Downs et al. (2019) failed to demonstrate a clear impact of culling using simple univariate analyses comparing TB trends over time. Effects of culling were only demonstrated by comparing TB incidence rates in cull areas (>250 km^2 in size), each matched to ten comparison areas, using multivariate analyses which controlled for TB history, herd size, type and several other covariates. Similarly, analyses of the RBCT involved randomly selected areas, large sample sizes and multivariable analyses

which controlled for many potentially confounding factors (Donnelly et al., 2007).

Statistically rigorous studies to investigate the impact of badger vaccination would ideally involve large, replicated areas with matched controls. In England, badger vaccination has typically take place over relatively small areas (Benton et al., 2020), with large scale culling across much of the endemic TB area limiting opportunities for unmanaged control areas. Future analyses could therefore investigate the impacts of badger vaccination in areas which have already been subjected to culling, as in Martin et al. (2020). Cattle TB incidence in vaccination areas could be compared to periods prior to vaccination as part of a 'difference in differences" approach which is being used in investigate further culling impacts in England (Birch et al., 2024). Alternatively, the small-scale nature of vaccination may require a herd-based approach to investigate the impact of badger vaccination alongside other herd level risk factors, such as herd size or biosecurity practices. Such an approach could also account for varying badger vaccination effort, and in the long run, cattle vaccination when this becomes available. Modelling studies provide an alternative approach to measure the effectiveness of badger vaccination trials where they are informed by real field data. For example, Chang et al. (2025) estimates that the badger vaccination in Kilkenny in Ireland in combination with cattle measures has significantly reduced bTB transmission in the area, but is unlikely to lead to eradication, in part due to due to persistence within a subset of high-risk areas or herds.

2. Public attitudes towards badger vaccination

Bovine TB management is an emotive and contentious issue and there are strong, often polarised views on control measures, particularly those involving badgers (Cassidy, 2012). Badger vaccination involves multiple stakeholders, including farmers, vets, government staff, along with NGOs and volunteers who have played a significant role in its early deployment (Benton et al., 2020). Understanding the views of stakeholders is therefore important for determining potential drivers and barriers for future roll-out.

A large survey of more than 300 farmers in the BVDP and four other areas in England provides some insights into their views on badger vaccination as a TB control tool (Enticott et al., 2012, 2014, 2020; Maye et al., 2013). Most farmers interviewed (61 %) considered badger vaccination to be less effective than culling at controlling TB. However, 41 % of farmers viewed badger vaccination as an 'acceptable method of disease control', with a similar number (45 %) believing that it would reduce TB in cattle (Enticott et al., 2012, 2014; Maye et al., 2013). Views of vaccination were more positive in the BVDP than in the four areas where no vaccination was taking place. This suggested that familiarity with the process may lead to more positive views on vaccination, although in all areas farmer perceptions became more negative over time from 2010 to 2014 (Enticott et al., 2020). Changes in farm biosecurity within badger vaccination areas have also been investigated, to determine if more active control of the disease in wildlife changed attitudes towards farm practices. While there was little evidence that biosecurity practices changed because of badger vaccination, farmers within the BVDP area were more likely to start fencing off badger latrines or setts than those outside of the area (Enticott et al., 2020).

Views on badger vaccination are also reported by 14 farmers interviewed at the National Trust Killerton Estate (vaccinated from 2010 to 2014), the majority of whom believed that it would have positive disease control benefits, but that culling would be more effective, and gave an overall impression of 'tolerance, rather than optimism' in relation to badger vaccination (Warren et al., 2013). Clarke et al. (2022) conducted a survey of 280 farmers in the Burren in the West of Ireland, and a small number of farmers ($n < 10$) used the free text at the end of the survey to vocalise support for vaccination "encourage vaccination of the badger, eliminate the chances of passing it on to the cattle". In England, Chivers et al. (2022) conducted a series of participatory workshops with farmers to discuss four different scenarios for future badger vaccination roll-out; 1) government led vaccination; 2) a science led trial of vaccination; 3) farmer led vaccination in post cull areas; and 4) a combined approach with farmers vaccinating both badgers and cattle. In all workshops there was broad repeated rejection of badger vaccination with most sentiments expressed being described as negative for all scenarios, although the scientific trial option received the most positive response (Clarke et al., 2022).

Multiple factors likely contribute to the negative views of badger vaccination by farmers including the limited evidence for positive impacts on TB in cattle and concern that vaccination may disturb badger populations and have negative disease outcomes (Enticott et al., 2014; Benton et al., 2020). Many farmers believe that badger vaccination is simply impractical (Maye et al., 2013; Warren et al., 2013; Benton et al., 2020), particularly those with experience of trapping badgers for culling (Chivers et al., 2022). Negative views of vaccination also stem from farmer beliefs about nature, with many of the view that badger populations need to be controlled, and that high numbers represent an imbalance that requires correcting (Enticott et al., 2014; Chivers et al., 2022). Enticott et al. (2020) also suggests that badger vaccination lacks 'practice similarity' compared to the vaccination of livestock, with concerns over the lack of vaccine efficacy in badgers which were already infected with TB, and a belief that the vaccine would only work if 100 % of badgers were vaccinated.

Vets are also key stakeholders in bTB control, and a recent study by (Kenny et al., 2024) provides insight into the views of private veterinary practitioners in badger vaccination in Ireland. Some vets had a positive view of badger vaccination stating it showed "good promise", but others questioned its effectiveness and current scale, with a preference for badger culling by some vets, particularly in areas where vaccination was viewed to have failed to control TB. A lack of information about the badger vaccination campaign in Ireland was also highlighted by some vets in the study.

Those working with NGOs to deliver badger vaccination cite several motivations for their involvement in the process, including a desire to control TB or demonstrate the effectiveness of vaccination, professional development, or building relationships with the farming community (Benton et al., 2020). However, they also cite several barriers including limited funding, low levels of participation and low confidence in effectiveness and practicality among landowners (Benton et al., 2020). The largely negative view of badger vaccination in the farming community is at odds with broader public perceptions. For example, 61 % of responses to a public consultation on proposed methods for controlling TB in badgers in 2010 were in favour of badger vaccination and opposed to culling (Defra, 2011). Dicks et al. (2021) analysed social media posts following the UK Government announcement that badger vaccination would gradually replace culling as the primary method of wildlife disease control in England. They found that 98 % of posts relating to vaccination were favourable, compared to only 1 % in support of badger culling. Both studies mentioned here likely represent a biased sample which is unrepresentative of the wider population, but nevertheless the results are in stark contrast to those from surveys of farmer views on vaccination (Enticott et al., 2012).

Analyses of options to control TB in badgers based on a utilitarian approach, considering human wellbeing and animal welfare, identify badger vaccination as the preferred option compared to either badger culling or doing nothing (McCulloch and Reiss, 2017), assuming that vaccination will yield a 12.5 % reduction in bTB, compared to 19 % for culling. The preference for vaccination in this analysis is related to the higher estimated welfare benefits in badgers, combined with greater support among the non-farming public for vaccination, relative to badger culling. The polarised views of stakeholders on how to control TB risks from badgers are likely due to a combination of factors, including how badgers and control methods are represented in the media (Cassidy, 2012). In a detailed analysis of press coverage of badger vaccination, (Naylor et al., 2017), found that the issue was often presented as 'science

vs practicality' and that because the evidence is disputed and reported inconsistently this causes both confusion and misinterpretation. The authors also suggest that while a significant proportion of articles (70 %) contain positive statements about vaccination, the issue is often framed as "badger vaccination vs badger culling" and such "*emotive framings*" fuel further controversy.

3. Discussion

The evidence to date indicates that badger vaccination has the potential to reduce *M. bovis* infection in wild badger populations and so could contribute to a wider strategy for controlling bTB. Multiple experimental trials on captive badgers have demonstrated a protective effect of BCG vaccination against *M. bovis,* although protection is typically incomplete, with most vaccinated badgers becoming infected but exhibiting marked reductions in measures of disease. This is comparable with BCG challenge studies in other species (Buddle et al., 2018) and is likely due to the very high doses of *M. bovis* administered, to generate consistent infection and quantifiable pathology over a relatively short (12–17 week) period (Corner et al., 2008; Chambers et al., 2014). The injectable BadgerBCG vaccine is licenced in the UK underpinned by evidence that the vaccine reduces the severity and progression of disease, as well as reducing excretion of *M. bovis* from infected badgers (Chambers et al., 2011; Brown et al., 2013). Despite the incomplete protection afforded in a controlled captive setting, field trials have consistently demonstrated that vaccination with BCG significantly reduces the likelihood that badgers will become infected with *M. bovis* under natural field conditions. As BCG is a prophylactic vaccine, it is assumed that the vaccine is unlikely have any beneficial effects in individuals which are already infected (Andersen, 2007). BCG is generally viewed as a safe vaccine with minimal side effects or welfare issues (Buddle et al., 2018) and studies on the injectable BCG vaccine in badgers confirm this, with no significant reactions to the vaccine, no excretion of BCG and no changes in behaviour which could result in negative disease outcomes.

Badger populations are highly variable, with density and TB prevalence varying markedly both at the landscape scale (Judge et al., 2017; Schroeder et al., 2020), and within populations, where infection is often patchy and clustered (Delahay et al., 2000; Woodroffe et al., 2005). Where badgers are free of TB, BCG vaccination should reduce the likelihood of new infections, from either badgers or from cattle, and act as a defence against disease becoming established. Where badger populations are already infected, vaccination will act to reduce the number of individuals susceptible to infection, which should reduce TB prevalence over time. This is supported by multiple modelling studies which predict that vaccination will lead to a decline in TB prevalence in badger populations with pre-existing infection if deployment is sufficiently extensive in time and space. However, studies investigating the effects of badger vaccination in the field to date come from only two locations, which represent only a narrow portion of the range of badger densities and TB prevalence found across Great Britain and Ireland While there is evidence of reduced disease incidence in both studies, it is difficult to demonstrate declining prevalence in live tested badgers, in part because of the low sensitivity of the available tests. However, testing of euthanised badgers in Ireland found clear patterns consistent with reductions in overall levels of TB infection at the population level. Further field studies of vaccination outcomes in badgers in a wider range of environments, along with new approaches for testing live badgers for infection (Smith et al., 2021) or the testing of environmental samples for *M. bovis* (Murphy et al., 2020), may help further demonstrate the effects of vaccination on TB in badgers under field conditions.

Given the cost and practical challenges of testing badgers in the field, simulation modelling remains a valuable tool for evaluating the likely impact of vaccination under a range of conditions. Relatively modest levels of vaccine coverage (>30 %) are predicted to lead to declines in prevalence in badger populations, although it seems likely that much higher levels of coverage would be needed to rapidly reduce TB in badger populations. Whether vaccination leads to eradication in badgers may also depend on which cattle control measures are in place, as some studies suggest infection in both species is required for $R > 1$ and that infection in one species alone may be insufficient to maintain the disease (Aznar et al., 2022; Bouchez-Zacria et al., 2023).

Simulation models have evaluated badger vaccination under differing population densities and levels of coverage, but one area which has not been investigated is how badger density and vaccine coverage interact with TB prevalence to determine disease control outcomes. For example, there may be certain cut-off points where density or prevalence is so high that vaccination would have only a limited impact on transmission, or where the coverage required to have an impact is unachievable. These challenges have been demonstrated in modelling studies of vaccination against rabies in high density fox populations (Smith and Wilkinson, 2003) and in field studies of rabies in raccoons (Ramey et al., 2008). How the spatial scale of vaccination operations interacts with these factors is also unclear. For example, do vaccination areas need to be a minimum size to result in disease control benefits? Policy makers and wildlife managers have limited information on badger density and TB prevalence, and it is unclear in which situations vaccination would be most advantageous, relative to other control methods. Further modelling studies considering a broader range of situations could help to inform decisions and direct management, as could the collection of better data to improve such models going forward

Badger vaccination programmes conducted to date in England demonstrate that large numbers of badgers can be vaccinated, and high levels of trapping efficiency and apparent vaccination coverage can be achieved (Benton et al., 2020). An increase in badger vaccination in future years will potentially see badgers trapped in highly disturbed populations transitioning from several years of culling, which contrasts with previous vaccination programmes which have largely taken place in high density undisturbed badger populations. Although initial comparisons between vaccination operations in culled and unculled populations demonstrated similar levels of trapping efficiency in government programmes (Benton et al., 2023), these data are based on a single culled area. In Ireland, vaccination is regularly conducted in post-cull badger populations but there are no published studies yet analysing trapping data from these projects. Given the potential challenges associated with trapping culled populations (see Benton et al. (2023), further research into the effectiveness of trapping operations in heavily culled populations are needed. These field studies and model outputs (Smith and Budgey, 2021) appear to suggest that vaccination in a post-culled badger population is effective, indicating that roll-out of vaccination soon after badger culling has ceased may be preferable to delaying vaccination until badger populations have recovered.

One key evidence gap associated with badger vaccination is the duration of immunity (DOI) following vaccination. Captive trials are typically short, with badgers challenged 3–4 months post vaccination, and then euthanised 3–4 months later. Field trials to date have involved annual vaccination of all trapped badgers (Chambers et al., 2011), and this is the approach taken in wider vaccine deployment programmes; not least in order to vaccinate each year's new birth cohort. In humans the DOI for BCG can range from several years to several decades, but in some cases can be much shorter. Studies of BCG vaccination of brushtail possums (*Trichosurus vulpecula*) have shown evidence of protection up to 28 months post vaccination, which was the maximum time span measured (Tompkins et al., 2013). Badgers typically live for 3–5 years (Roper, 2010), so a DOI of several years could be equivalent to lifelong immunity in most individuals. A better understanding of DOI in badgers could reduce the need for repeated vaccination and hence substantially reduce costs, although this would need to be balanced against the benefits of vaccinating new cubs each year and the potential for declining vaccine immunity over time.

Arguably the largest evidence gap relating to use of badger vaccination as a management tool is the uncertainty over its effect on TB

incidence in cattle. If vaccination reduces transmission in badgers, this will reduce prevalence in the badger population, and it follows that fewer infected badgers should reduce opportunities for transmission to cattle. This is supported by modelling studies predicting a reduction in bTB incidence following badger vaccination (Smith et al., 2012). Results from a study in Ireland indicating that changing from badger culling to badger vaccination in four counties was not associated with an unacceptable increase in cattle TB incidence (i.e vaccination was not inferior), also provide field evidence for the effectiveness of vaccination as a tool to control bTB in cattle (Martin et al., 2020). The recent work of Chang et al. (2025), however should provide a note of caution, as their results suggest that badger vaccination combined with existing cattle controls may be unlikely to eradicate TB from the cattle population. This result is partly due to the spatially variable role of badgers a source of infection, but also due to the significant contribution of cattle-to-cattle transmission in disease persistence and spread. This suggests that a combination of TB control measures are likely needed to achieve eradication, tailored to the local disease situation.

. Further studies into the effectiveness of badger vaccination at controlling TB in cattle in Ireland and the UK are therefore needed. As TB risk in cattle is influenced by a range of factors (Broughan et al., 2016), studies to evaluate the impacts of badger vaccination will need to have sufficient statistical power to control for these potential confounders. Demonstrating impacts of vaccination in England will be further complicated by the varying and often unquantified role that badgers play in *M. bovis* transmission, along with the fact that badger populations have been culled across large areas of England. Ideally, studies investigating the impacts of badger vaccination on bTB would cover multiple randomly selected areas, such that any results could be applicable to the broad range of potential future scenarios (badger density, TB prevalence, cattle population etc) where badger vaccination could be deployed in the future. However, given the scale and cost of such an undertaking, an initial and shorter-term priority might be to define a statistical approach to evaluate the impacts of the localised and piecemeal badger vaccination that has been conducted to date.

Given the effort involved in trapping badgers for vaccination, delivery of the vaccine in bait remains an attractive alternative, as oral vaccines have proved effective at controlling other infectious diseases in wildlife populations (Cross et al., 2007). There has been some progress in developing a bait and delivery method for oral badger BCG vaccine (Gowtage et al., 2017; Robertson et al., 2022). Despite evidence of protection from direct orally administered BCG in the field (Gormley et al., 2021), the variable and inconsistent protection afforded by oral vaccination through baits in challenge studies has so far hindered progress in developing a bait delivered oral vaccine that could be taken forward to licensing, and no work is currently being undertaken in this area. It may be that demonstrating vaccine efficacy for an oral BCG vaccine within an edible bait is simply not possible in a captive study involving an unnaturally high challenge. Alternative approaches involving field trials to demonstrate vaccine efficacy have been conducted in other species such as cattle (Bayissa et al., 2021). A field study of an oral badger vaccine might demonstrate whether current vaccine baits provide sufficient protection against a more natural challenge and therefore have the potential to produce disease control benefits.

Reviewing the social science literature has highlighted that badger vaccination is largely viewed negatively by members of the farming community The reasons for this are complex, with concerns over the effectiveness and practicality of vaccination along with engrained perceptions of the role of badgers in the countryside, linked to a view that their numbers need to be managed by lethal control. Some of these concerns relate to genuine gaps in the evidence, such as the uncertainty around impacts of badger vaccination on bTB, particularly relative to the larger evidence base on the impacts of badger culling (Bourne et al., 2007; Downs et al., 2019; Birch et al., 2024). However, some of this negativity may relate to how vaccination is presented in the press (Naylor et al., 2017), and a failure to communicate the evidence for disease control benefits in badger populations (Carter et al., 2012) and the high levels of vaccination coverage that can be achieved (Benton et al., 2020). Despite negative perceptions and gaps within the evidence base this review suggests that there is a significant body of evidence to support badger vaccination as an approach that could make a meaningful contribution to the control of TB in badgers and cattle. Evidence for the effectiveness of TVR in reducing TB in badgers, without disrupting their behaviour is also encouraging. Further options involving vaccination in combination with lethal control could also include vaccinating either pre or post cull, or in buffer areas surround culled populations. The current roll out of wider badger vaccination in England and Ireland provides opportunities to gather valuable data on the impacts on TB in badger and cattle populations, to learn practical lessons about large-scale vaccine deployment, and to explore means of gaining wider stakeholder engagement.

CRediT authorship contribution statement

N.M. Brotherton Peter: Writing – review & editing, Conceptualization. **Delahay Richard J.:** Writing – review & editing. **McDonald Robbie A.:** Writing – review & editing. **Chambers Mark:** Writing – review & editing. **Smith Graham C:** Writing – review & editing. **Robertson Andrew:** Writing – original draft, Conceptualization.

Declaration of Competing Interest

There is no significant conflict of interest to declare. It should be noted that several of the authors have been involved in government funded research in England into badger vaccination and have authored some of the key papers referenced within the review, although given that they are experts in this field this should be of no surprise to the journal. The lead author AR as of 09/23 is employed by DEFRA, although this review was written prior to this appointment while they were employed by Exeter University and Natural England.

References

Abdou, M., Frankena, K., O'Keeffe, J., Byrne, A.W., 2016. Effect of culling and vaccination on bovine tuberculosis infection in a European badger (Meles meles) population by spatial simulation modelling. Prev. Vet. Med. 125, 19–30.
Andersen, P., 2007. Vaccine strategies against latent tuberculosis infection. Trends Microbiol 15, 7–13.
Anderson, R., Trewhella, W., 1985. Population dynamics of the badger (Meles meles) and the epidemiology of bovine tuberculosis (Mycobacterium bovis). Philos. Trans. R. Soc. Lond. Ser. B, Biol. Sci. 310, 327–381.
APHA, 2010. Field Trial to Assess the Safety of Bacille Calmette Guerin (BCG) Vaccine Administered Parenterally to Badgers.
APHA, 2015. Badger Vaccine Deployment Project: Final lessons learned report.
APHA, 2016a. APHA report of examination for Mycobacterium bovis in badgers found dead within the Welsh Government Intensive Action Area (IAA) (OG0145/TBOG0146).
APHA, 2016b. A descriptive analysis of the effect of badger vaccination on the incidence of bovine tuberculosis in cattle within the Badger Vaccine Deployment Project area, using obervational data.
APHA, 2016c. Differences between bovine TB indicators in the IAA and the Comparison Area: First six years, 1st May 2010 to 30th April 2016.
Aznar, I., McGrath, G., Murphy, D., Corner, La.L., Gormley, E., Frankena, K., More, S.J., Martin, W., O'Keeffe, J., De Jong, M.C.M., 2011. Trial design to estimate the effect of vaccination on tuberculosis incidence in badgers. Vet. Microbiol. 151, 104–111.
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. Prev. Vet. Med. 149, 29–37.
Aznar, I., Frankena, K., More, S., Clegg, T., McGrath, G., O'Keeffe, J., Byrne, A., De Jong, M., 2022. Compute Bounds of Transmission Parameters of M.bovis in the Badger-Cattle System from Endemic Prevalences.
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., 2020. Protective effect of oral bcg and inactivated mycobacterium bovis vaccines in european badgers (Meles meles) experimentally infected with M. bovis. Front. Vet. Sci. 7.
Barlow, N.D., 1996. The ecology of wildlife disease control: simple models revisited. J. Appl. Ecol. 33, 303–314.
Bayissa, B., Sirak, A., Worku, A., Zewude, A., Zeleke, Y., Chanyalew, M., Gumi, B., Berg, S., Conlan, A., Hewinson, R., Wood, J.L.N., Vordermeier, H.M., Ameni, G., 2021. Evaluation of the efficacy of BCG in protecting against contact challenge with

bovine tuberculosis in holstein-friesian and zebu crossbred calves in ethiopia. Front. Vet. Sci. 8, 702402.
Bentil, D., Murray, J., 1993. Modelling bovine tuberculosis in badgers. J. Anim. Ecol. 239–250.
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 Nat. 2, 761–775.
Benton, C.H., Phoenix, J., Robertson, A., Delahay, R.J., 2023. Vaccinating badgers in a post-cull landscape; insights from the field. Ecol. Solut. Evid. 4, e12208.
Biek, R., O'Hare, A., Wright, D., Mallon, T., McCormick, C., Orton, R.J., McDowell, S., Trewby, H., Skuce, R.A., Kao, R.R., 2012. Whole genome sequencing reveals local transmission patterns of mycobacterium bovis in sympatric cattle and badger populations. PLoS Path 8, e1003008.
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. Sci. Rep. 14, 4849.
Blanco Vázquez, C., Prieto, M., Barral, M., Juste, R.A., Lesellier, S., Salguero, F.J., Davé, D., Martínez, I.Z., de Garnica García, M.G., Casais, R., Balseiro, A., 2020. Local Lung Immune Response to Mycobacterium bovis Challenge after BCG and M. bovis Heat-Inactivated Vaccination in European Badger (Meles meles). Pathogens 9, 456.
Bouchez-Zacria, M., Ruette, S., Richomme, C., Lesellier, S., Payne, A., Boschiroli, M.-L., Courcoul, A., Durand, B., 2023. Analysis of a multi-type resurgence of Mycobacterium bovis in cattle and badgers in Southwest France, 2007-2019. Vet. Res. 54, 41.
Bourne, J., Donnelly, C., Cox, D., Gettinby, G., Morrison, I., Woodroffe, R., 2007. Bovine TB: The Scientific Evidence. A Science Base for a Sustainable Policy to Control TB in Cattle. An Epidemiological Investigation into Bovine Tuberculosis. The Final Report of the Independent Scientific Group on Cattle TB. In, London.
Brewer, T.F., 2000. Preventing tuberculosis with bacillus Calmette-Guérin vaccine: a meta-analysis of the literature. Clin. Infect. Dis. 31 (3), S64–S67.
Broughan, J., Judge, J., Ely, E., Delahay, R., Wilson, G., Clifton-Hadley, R., Goodchild, A., Bishop, H., Parry, J., Downs, S., 2016. A review of risk factors for bovine tuberculosis infection in cattle in the UK and Ireland. Epidemiol. Infect. 1–28.
Broughan, J.M., Downs, S.H., Crawshaw, T.R., Upton, P.A., Brewer, J., Clifton-Hadley, R. S., 2013. Mycobacterium bovis infections in domesticated non-bovine mammalian species. Part 1: Review of epidemiology and laboratory submissions in Great Britain 2004–2010. Vet. J. 198, 339–345.
Brown, E., Cooney, R., Rogers, F., 2013. Veterinary guidance on the practical use of the BadgerBCG tuberculosis vaccine. Practice 35, 143–146.
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. Front. Vet. Sci. 5.
Byrne, A.W., O'Keeffe, J., Green, S., Sleeman, D.P., Corner, L.A.L., Gormley, E., Murphy, D., Martin, S.W., Davenport, J., 2012b. Population estimation and trappability of the european badger (Meles meles): implications for tuberculosis management. PLOS ONE 7, e50807.
Byrne, A.W., O'Keeffe, J., Sleeman, D.P., Davenport, J., Martin, S.W., 2012a. Factors affecting European badger (Meles meles) capture numbers in one county in Ireland. Prev. Vet. Med.
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. Transbound. Emerg. Dis. 2024, 8875146.
Carter, S.P., Delahay, R.J., Smith, G.C., Macdonald, D.W., Riordan, P., Etherington, T.R., Pimley, E.R., Walker, N.J., Cheeseman, C.L., 2007. Culling-induced social perturbation in Eurasian badgers Meles meles and the management of TB in cattle: an analysis of a critical problem in applied ecology. Proc. R. Soc. B 274, 2769–2777.
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., McDonald, R.A., 2012. BCG vaccination reduces risk of tuberculosis infection in vaccinated badgers and unvaccinated badger cubs. PloS One 7, e49833.
Cassidy, A., 2012. Vermin, victims and disease: UK framings of badgers in and beyond the bovine TB controversy. Soc. Rural. 52, 192–214.
Chambers, M.A., Rogers, F., Delahay, R.J., Lesellier, S., Ashford, R., Dalley, D., Gowtage, S., Davé, D., Palmer, S., Brewer, J., Crawshaw, T., Clifton-Hadley, R.S., Carter, S.P., Cheeseman, C., Hanks, C., Murray, A., Palphramand, K., Pietravalle, S., Smith, G.C., Tomlinson, A.J., Walker, N., Wilson, G.J., Corner, L.A.L., Rushton, S., Shirley, M.D.F., Gettinby, G., McDonald, R.A., Hewinson, G., 2011. Bacillus Calmette-Guérin vaccination reduces the severity and progression of tuberculosis in badgers. Proc. R. Soc. B 278, 1913–1920.
Chambers, M.A., Carter, S.P., Wilson, G.J., Jones, G., Brown, E., Hewinson, R.G., Vordermeier, M., 2014. Vaccination against tuberculosis in badgers and cattle: an overview of the challenges, developments and current research priorities in Great Britain. Vet. Rec. 175, 90–96.
Chambers, M.A., Aldwell, F., Williams, G.A., Palmer, S., Gowtage, S., Ashford, R., Dalley, D.J., Davé, D., Weyer, U., Salguero, F.J., 2017. The effect of oral vaccination with Mycobacterium bovis BCG on the development of tuberculosis in captive European badgers (Meles meles). Front. Cell. Infect. Microbiol. 7.
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. Front. Vet. Sci. 10.
Chang, Y., Widgren, S., de Jong, M.C.M., Tratalos, J.A., More, S.J., Hartemink, N., 2025. 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. Prev. Vet. Med. 235, 106386.
Chivers, C., Maye, D., Enticott, G., Lenormand, T., Tomlinson, S., 2022. Explor. Farmer Attitudes Towards Vaccin. Badgers Bov. Tuberc.
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. Front. Vet. Sci. 9.
Conlan, A.J.K., McKinley, T.J., Karolemeas, K., Pollock, E.B., Goodchild, A.V., Mitchell, A.P., Birch, C.P.D., Clifton-Hadley, R.S., Wood, J.L.N., 2012. Estimating the Hidden Burden of Bovine Tuberculosis in Great Britain. PLoS Comp. Biol. 8, e1002730.
Corner, L.A.L., Costello, E., Lesellier, S., O'Meara, D., Sleeman, D.P., Gormley, E., 2007. Experimental tuberculosis in the European badger (Meles meles) after endobronchial inoculation of Mycobacterium bovis: I. Pathology and bacteriology. Res. Vet. Sci. 83, 53–62.
Corner, L.A.L., Costello, E., Lesellier, S., O'Meara, D., Gormley, E., 2008. Vaccination of European badgers (Meles meles) with BCG by the subcutaneous and mucosal routes induces protective immunity against endobronchial challenge with Mycobacterium bovis. Tuberculosis 88, 601–609.
Corner, L.A.L., Costello, E., O'Meara, D., Lesellier, S., Aldwell, F.E., Singh, M., Hewinson, R.G., Chambers, Ma, Gormley, E., 2010. Oral vaccination of badgers (Meles meles) with BCG and protective immunity against endobronchial challenge with Mycobacterium bovis. Vaccine 28, 6265–6272.
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, 4972–4978.
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, e45833.
Cross, M.L., Buddle, B.M., Aldwell, F.E., 2007. The potential of oral vaccines for disease control in wildlife species. Vet. J. 174, 472–480.
DAFM, 2021. Bovine TB Eradication Strategy: A roadmap to reduce bovine TB and drive towards eradication 2021-2030.
Defra, 2011. Bovine tuberculosis: The government's approach to tackling the disease and consultation on a badger control policy—Summary of consultation responses. London.
Defra, 2020. Next Steps for the Strategy for Achieving Bovine Tuberculosis Free Status for England: The Government's Response to the Strategy Review, 2018. London, UK.
Delahay, R.J., Langton, S., Smith, G.C., Cheeseman, C.L., 2000. The spatio-temporal distribution of Mycobacterium bovis (bovine tuberculosis) infection in a high-density badger population.
Delahay, R.J., Wilson, G.J., Smith, G.C., Cheeseman, C.L., 2003. Vaccinating badgers (Meles meles) against Mycobacterium bovis: the ecological considerations. Vet. J. 166, 43–51.
Delahay, R.J., Smith, G.C., Barlow, A.M., Walker, N., Harris, A., Clifton-Hadley, R.S., Cheeseman, C., 2007. Bovine tuberculosis infection in wild mammals in the South-West region of England: A survey of prevalence and a semi-quantitative assessment of the relative risks to cattle. Vet. J. 173, 287–301.
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, 314.
Donnelly, C.A., Woodroffe, R., Cox, D.R., Bourne, J., Gettinby, G., Le Fevre, A.M., McInerney, J.P., Morrison, W.I., 2003. Impact of localized badger culling on tuberculosis incidence in British cattle. Nature 426, 834–837.
Donnelly, C.A., Wei, G., Johnston, W.T., Cox, D.R., Woodroffe, R., Bourne, F.J., Cheeseman, C.L., Clifton-Hadley, R.S., Gettinby, G., Gilks, P., Jenkins, H.E., Le Fevre, A.M., McInerney, J.P., Morrison, W.I., 2007. Impacts of widespread badger culling on cattle tuberculosis: concluding analyses from a large-scale field trial. Int. J. Infect. Dis. 11, 300–308.
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. Sci. Rep. 9, 14666.
Enticott, G., Maye, D., Ilbery, B., Fisher, R., Kirwan, J., 2012. Farmers' confidence in vaccinating badgers against bovine tuberculosis. Vet. Rec. 170, 204-204.
Enticott, G., Maye, D., Fisher, R., Ilbery, B., Kirwan, J., 2014. Badger vaccination: dimensions of trust and confidence in the governance of animal disease. Environ. Plan. A 46, 2881–2897.
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, 1065–1075.
Fine, A.E., Bolin, C.A., Gardiner, J.C., Kaneene, J.B., 2011. A study of the persistence of Mycobacterium bovis in the environment under natural weather conditions in Michigan, USA. Vet. Med. Int. 2011.
Foyle, K., Delahay, R., Massei, G., 2010. Isolation of Mycobacterium bovis from a feral wild boar (Sus scrofa) in the UK. Vet. Rec. 166, 663.
Godfray, C., Donnelly, C.A., Hewinson, G., Winter, M., Wood, J., 2018. Bovine TB strategy review. London: Defra.
Gormley, E., Ní, Bhuachalla, D., 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, e0168851.
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., 2021. Protective immunity against tuberculosis in a free-living badger population vaccinated orally with Mycobacterium bovis Bacille Calmette–Guérin. Transbound. Emerg. Dis. N./a.
Gortázar, C., Delahay, R.J., McDonald, R.A., Boadella, M., Wilson, G.J., Gavier-Widen, D., 2012. The status of tuberculosis in European wild mammals. Mammal. Rev. 42.
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, 987–992.
Griffin, J., Williams, D., Kelly, G., Clegg, T., O'boyle, I., Collins, J., More, S., 2005. The impact of badger removal on the control of tuberculosis in cattle herds in Ireland. Prev. Vet. Med. 67, 237–266.
Hardstaff, J.L., Bulling, M.T., Marion, G., Hutchings, M.R., White, P.C.L., 2013. Modelling the impact of vaccination on tuberculosis in badgers. Epidemiol. Infect. 141, 1417–1427.
Jenkins, H.E., Woodroffe, R., Donnelly, C.A., 2010. The duration of the effects of repeated widespread badger culling on cattle tuberculosis following the cessation of culling. PLoS One 5, e9090.
Judge, J., Wilson, G.J., Macarthur, R., McDonald, R.A., Delahay, R.J., 2017. Abundance of badgers (Meles meles) in England and Wales. Sci. Rep. 7.
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, e19349.
Kenny, U., Finn, S., Barrett, D., 2024. Private veterinarians' views of the Irish bovine TB eradication programme. Res. Vet. Sci. 173, 105246.
Krebs, J., 1997. Bovine tuberculosis in cattle and badgers. Ministry of Agriculture, Fisheries and Food, London.
Lesellier, S., Palmer, S., Dalley, D.J., Davé, D., Johnson, L., Hewinson, R.G., Chambers, M.A., 2006. The safety and immunogenicity of Bacillus Calmette-Guérin (BCG) vaccine in European badgers (Meles meles). Vet. Immunol. Immunopathol. 112, 24–37.
Lesellier, S., Corner, L., Costello, E., Lyashchenko, K., Greenwald, R., Esfandiari, J., Singh, M., Hewinson, R.G., Chambers, M., Gormley, E., 2009. Immunological responses and protective immunity in BCG vaccinated badgers following endobronchial infection with Mycobacterium bovis. Vaccine 27, 402–409.
Lesellier, S., Palmer, S., Gowtage-Sequiera, S., Ashford, R., Dalley, D., Davé, D., Weyer, U., Salguero, F.J., Nunez, A., Crawshaw, T., Corner, La.L., Hewinson, R.G., Chambers, M.A., 2011. Protection of Eurasian badgers (Meles meles) from tuberculosis after intra-muscular vaccination with different doses of BCG. Vaccine 29, 3782–3790.
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., Monchâtre-Leroy, E., Boué, F., Chambers, M.A., Richomme, C., 2019. Detection of live M. bovis BCG in tissues and IFN-γresponses in European badgers (Meles meles) vaccinated by oropharyngeal instillation or directly in the ileum. BMC Vet. Res. 15.
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, 782.
Mähl, P., Cliquet, F., Guiot, A.-L., Niin, E., Fournials, E., Saint-Jean, N., Aubert, M., Rupprecht, C.E., Gueguen, S., 2014. Twenty year experience of the oral rabies vaccine SAG2 in wildlife: a global review. Vet. Res. 45 (1).
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). Prev. Vet. Med. 179, 105004.
Maye, D., Enticott, G., Ilbery, B., Fisher, R., Kirwan, J., 2013. Assessing farmer confidence in badger vaccination: some findings from a survey of cattle farmers in England. J. Rural Community Dev. 8.
McCulloch, S.P., Reiss, M.J., 2017. Bovine tuberculosis and badger Culling in England: a utilitarian analysis of policy options. J. Agric. Environ. Ethics 30, 511–533.
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. Vet. Rec., e248
Murphy, A.R.J., Travis, E.R., Hibberd, V., Porter, D., Wellington, E.M.H., Fenwick, B., 2020. Evaluation of a fecal shedding test to detect badger social groups infected with mycobacterium bovis. J. Clin. Microbiol. 59 e01226-01220.
Murphy, D., Costello, E., Aldwell, F.E., Lesellier, S., Chambers, M.A., Fitzsimons, T., Corner, L.A., Gormley, E., 2014. Oral vaccination of badgers (Meles meles) against tuberculosis: comparison of the protection generated by BCG vaccine strains Pasteur and Danish. Vet. J. 200, 362–367.
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. Soc. Rural. 57, 3–22.
Ní Bhuachalla, D., Corner, L.A., More, S.J., Gormley, E., 2014. 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. Vet. Med.: Res. Rep. 27–38.
Palmer, M.V., Thacker, T.C., Waters, W.R., Gortázar, C., Corner, L.A.L., 2012. Mycobacterium bovis: a model pathogen at the interface of livestock, wildlife, and humans. Vet. Med. Int. 2012, 1–17.
Ramey, P.C., Blackwell, B.F., Gates, R.J., Slemons, R.D., 2008. Oral rabies vaccination of a northern Ohio raccoon population: relevance of population density and prebait serology. J. Wildl. Dis. 44, 553–568.
Redpath, S.H., Marks, N.J., Menzies, F.D., O'Hagan, M.J., Wilson, R.P., Smith, S., Magowan, E.A., McClune, D.W., Collins, S.F., McCormick, C.M., 2023. Impact of test, vaccinate and remove protocol on home ranges and nightly movements of badgers in a medium density population. Sci. Rep. 13, 2592.
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. Prev. Vet. Med. 206.
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. Comp. Immunol., Microbiol. Infect. Dis. 35, 277–287.
Roper, T., 2010. Badger. HarperCollins UK.
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. J. Appl. Ecol. 59, 210–222.
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. Ir. Vet. J. 76, 32.
Scanlon, M., Quinn, P., 2000. The survival of Mycobacterium bovis in sterilized cattle slurry and its relevance to the persistence of this pathogen in the environment. Ir. Vet. J. 53, 412–415.
Schiller, I., Oesch, B., Vordermeier, H.M., Palmer, M.V., Harris, B.N., Orloski, K.A., Buddle, B.M., Thacker, T.C., Lyashchenko, K.P., Waters, W.R., 2010. Bovine tuberculosis: a review of current and emerging diagnostic techniques in view of their relevance for disease control and eradication. Transbound. Emerg. Dis. 57, 205-220.
Schroeder, P., Hopkins, B., Jones, J., Galloway, T., Pike, R., Rolfe, S., Hewinson, G., 2020. Temporal and spatial Mycobacterium bovis prevalence patterns as evidenced in the All Wales Badgers Found Dead (AWBFD) survey of infection 2014–2016. Sci. Rep. 10, 15214.
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. Prev. Vet. Med. 183, 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. Eur. J. Wildl. Res. 67, 86.
Smith, G., Wilkinson, D., 2003. Modeling control of rabies outbreaks in red fox populations to evaluate culling, vaccination, and vaccination combined with fertility control. J. Wildl. Dis. 39, 278–286.
Smith, G., Budgey, R., Delahay, R., 2013. A simulation model to support a study of test and vaccinate or remove (TVR) in Northern Ireland.
Smith, G.C., Budgey, R., 2016. Simulations of the effect of badger vaccination on bovine tuberculosis in badgers and cattle within the IAA.
Smith, G.C., Budgey, R., 2021. Simulating the next steps in badger control for bovine tuberculosis in England. PLOS ONE 16, e0248426.
Smith, G.C., Cheeseman, C.L., 2002. A mathematical model for the control of diseases in wildlife populations: culling, vaccination and fertility control. Ecol. Model. 150, 45–53.
Smith, G.C., Delahay, R.J., 2018. Modeling as a decision support tool for bovine TB control programs in wildlife. Front. Vet. Sci. 5.
Smith, G.C., Cheeseman, C.L., Wilkinson, D., Clifton-Hadley, R.S., 2001. A model of bovine tuberculosis in the badger Meles meles: the inclusion of cattle and the use of a live test. J. Appl. Ecol. 38, 520–535.
Smith, G.C., McDonald, R.A., Wilkinson, D., 2012. Comparing badger (Meles meles) management strategies for reducing tuberculosis incidence in cattle. PloS One 7, e39250.
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, e0167206.
Smith, G.C., Barber, A., Breslin, P., Birch, C., Chambers, M., Dave, D., Hogarth, P., Gormley, E., Lesellier, S., Balseiro, A., Budgey, R., 2022. Simulating partial vaccine protection: BCG in badgers. Prev. Vet. Med. 204, 105635.
Smith, G.G., Richards, M.S., Clifton-Hadley, R.S., Cheeseman, C.L., 1995. Modelling bovine tuberculosis in badgers in england: preliminary results. Mammalia 59, 639–650.
Southey, A., Sleeman, D.P.S., Lloyd, K., Dalley, D., Chambers, M.A., Hewinson, R.G., Gormley, E., 2001. Immunological responses of Eurasian badgers (Meles meles) vaccinated with Mycobacterium bovis BCG (bacillus calmette guerin). Vet. Immunol. Immunopathol. 79, 197–207.

Stuart, F.A., Mahmood, K.H., Stanford, J.L., Pritchard, D.G., 1988. Development of diagnostic tests for, and vaccination against, tuberculosis in Badgers. Mamm. Rev. 18, 74–75.
Tompkins, D.M., Buddle, B.M., Whitford, J., Cross, M.L., Yates, G.F., Lambeth, M.R., Nugent, G., 2013. Sustained protection against tuberculosis conferred to a wildlife host by single dose oral vaccination. Vaccine 31, 893–899.
von Rüden, S., Staubach, C., Kaden, V., Hess, R.G., Blicke, J., Kühne, S., Sonnenburg, J., Fröhlich, A., Teuffert, J., Moennig, V., 2008. Retrospective analysis of the oral immunisation of wild boar populations against classical swine fever virus (CSFV) in region Eifel of Rhineland-Palatinate. Vet. Microbiol. 132, 29–38.
Ward, A.I., Smith, G.C., Etherington, T.R., Delahay, R.J., 2009. Estimating the risk of cattle exposure to tuberculosis posed by wild deer relative to badgers in England and Wales. J. Wildl. Dis. 45, 1104–1120.
Warren, M., Lobley, M., Winter, M., 2013. Farmer attitudes to vaccination and culling of badgers in controlling bovine tuberculosis. Vet. Rec. 173, 40-40.
White, P.C., Harris, S., 1995a. Bovine tuberculosis in badger (Meles meles) populations in southwest England: an assessment of past, present and possible future control strategies using simulation modelling. Philos. Trans. R. Soc. Lond. Ser. B: Biol. Sci. 349, 415–432.
White, P.C., Harris, S., 1995b. Bovine tuberculosis in badger (Meles meles) populations in southwest England: the use of a spatial stochastic simulation model to understand the dynamics of the disease. Philos. Trans. R. Soc. Lond. Ser. B: Biol. Sci. 349, 391–413.
Wilkinson, D., Smith, G., Delahay, R., Cheeseman, C., 2004. A model of bovine tuberculosis in the badger Meles meles: an evaluation of different vaccination strategies. J. Appl. Ecol. 41, 492–501.
Woodroffe, R., Donnelly, C.A., Johnston, W.T., Bourne, F.J., Cheesman, C.L., Clifton-Hadley, R.S., Cox, D.R., Gettinby, G., Hewinson, R.G., Fevre, A.M.L., McInerney, J.P., Morrison, W.I., 2005. Spatial association of Mycobacterium bovis infection in cattle and badgers Meles meles. J. Appl. Ecol. 42, 852–862.
Woodroffe, R., Donnelly, C.A., Ham, C., Jackson, S.Y., Moyes, K., Chapman, K., Stratton, N.G., Cartwright, S.J., 2017. Ranging behaviour of badgers Meles meles vaccinated with Bacillus Calmette Guerin. J. Appl. Ecol. 54, 718–725.
Woodroffe, R., Astley, K., 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 Nat. 6, 1960–1973.
Zuckerman, S.B., 1980. Badgers, Cattle, and Tuberculosis: Report to the Right Honourable Peter Walker. HM Stationery Office.