



HAL
open science

Advances and prospects for management of TB transmission between badgers and cattle

Gavin J. Wilson, Stephen P. Carter & Richard J. Delahay

► **To cite this version:**

Gavin J. Wilson, Stephen P. Carter & Richard J. Delahay. Advances and prospects for management of TB transmission between badgers and cattle. *Veterinary Microbiology*, 2011, 151 (1-2), pp.43. 10.1016/j.vetmic.2011.02.024 . hal-00701907

HAL Id: hal-00701907

<https://hal.science/hal-00701907>

Submitted on 28 May 2012

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Accepted Manuscript

Title: Advances and prospects for management of TB transmission between badgers and cattle

Authors: Gavin J. Wilson, Stephen P. Carter & Richard J. Delahay



PII: S0378-1135(11)00105-2
DOI: doi:10.1016/j.vetmic.2011.02.024
Reference: VETMIC 5191

To appear in: *VETMIC*

Please cite this article as: Wilson, G.J., Delahay, S.P.C.R.J., Advances and prospects for management of TB transmission between badgers and cattle, *Veterinary Microbiology* (2010), doi:10.1016/j.vetmic.2011.02.024

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

1 **Advances and prospects for management of TB transmission between badgers**
2 **and cattle**

3 Gavin J. Wilson*, Stephen P. Carter & Richard J. Delahay

4 The Food and Environment Research Agency, Woodchester Park, Tinkley Lane,
5 Nympsfield, Stonehouse, Gloucestershire GL10 3UJ, UK.

6 *Corresponding author: Tel 01453 861400, Fax 01453 860132, email
7 gavin.wilson@fera.gsi.gov.uk

8

9 **Abstract**

10 Bovine tuberculosis (bTB) is the most serious endemic disease facing the livestock
11 industry in the United Kingdom (UK) and Republic of Ireland (RoI), where its
12 management has been confounded by the presence of persistent infection in the
13 Eurasian badger (*Meles meles*). Field evidence suggests that the social structure of
14 badger populations can have an important influence on disease dynamics, and on the
15 outcome of management interventions. Recent, large-scale badger culling experiments
16 in the UK and RoI had complex epidemiological outcomes. In the UK, proactive
17 culling led to reduced bTB incidence in cattle herds inside culled areas, but a
18 temporary increase in adjacent areas. Reactive culling in response to herd breakdowns
19 was associated with an increase in the incidence of bTB in cattle. In contrast, badger
20 culling in RoI was reported to have only beneficial effects on bTB incidence in cattle.
21 The reasons for these differences are not clear. The complexity of the evidence base
22 for culling is highlighted by the different management approaches currently being
23 adopted by the different authorities of the UK and RoI.

24 It is generally accepted that a holistic approach to bTB management, which
25 targets both cattle and wildlife, is necessary. Consequently recent research activities

1 have also focussed on cattle and badger vaccines, and biosecurity on farms. This
2 paper describes recent advances in our understanding of the epidemiology of bTB in
3 badgers and the consequences of culling, and current research to develop approaches
4 for the vaccination of badgers, and methods of managing the risks of contact between
5 badgers and cattle in farm buildings.

6

7 **Keywords:** badger, bovine tuberculosis, wildlife reservoir, transmission, control,
8 management

9

10 **1. Introduction**

11 The eradication of bovine tuberculosis (bTB) from cattle in the UK and Republic of
12 Ireland (RoI) has been compromised by the presence of endemic infection in the
13 Eurasian badger (*Meles meles*). Since the early to mid 1970s when they were first
14 suspected to be sources of infection for cattle, badgers have been culled in both
15 countries under a variety of different strategies. Although badgers have been protected
16 in the UK and RoI since 1973 and 1976 respectively, culling has been employed since
17 1973 as the primary tool for targeting the reservoir of infection in wildlife, as a
18 complement to cattle-based controls (Krebs, 1997). In the areas of cattle herd
19 incidence of the UK, specifically parts of the south-west of England and Wales, an
20 initial decrease in the incidence of herd breakdowns provided some encouragement
21 that culling could be an effective management approach (Zuckerman, 1980).
22 Localised, intensive badger removal operations in England and RoI were also
23 accompanied by reported decreases in cattle herd breakdown incidence (Clifton-
24 Hadley et al., 1995; Ó Máirtín et al., 1998; Eves, 1999). However, since the late

1 1980s, the incidence of TB in cattle has risen against a background of statutory badger
2 culling in England and Wales (Krebs, 1997; <http://www.defra.gov.uk>).

3 Concerns over the increasing incidence and geographic spread of bTB in cattle
4 led in 1997 to the suspension of badger culling as a management policy in England
5 and Wales and the appointment of an independent advisory committee to MAFF
6 (Ministry of Agriculture, Fisheries and Food; Krebs, 1997), the predecessor to the
7 current responsible government department, Defra (Department for Environment,
8 Food and Rural Affairs). The committee recommended a range of scientific research,
9 including a field experiment to determine the efficacy of badger culling in reducing
10 bTB incidence in cattle. The UK government accepted most of the recommendations
11 and in 1998 an Independent Scientific Group on Cattle TB (ISG) was convened to
12 design and oversee the Randomised Badger Culling Trial (RBCT). In their final report
13 the ISG recommended a range of policy options focussing on more stringent cattle
14 control measures, and concluded that “badger culling cannot meaningfully contribute
15 to the future control of cattle TB in Britain” (Independent Scientific Group, 2007).
16 Despite being supported by numerous publications in peer-reviewed journals, the
17 ISG’s conclusions were not universally accepted (More et al., 2007;
18 [http://www.defra.gov.uk/foodfarm/farmanimal/diseases/atoz/tb/documents/badgersrep
19 ort-king.pdf](http://www.defra.gov.uk/foodfarm/farmanimal/diseases/atoz/tb/documents/badgersreport-king.pdf)). Nevertheless, a subsequent inquiry by a House of Commons Select
20 Committee acknowledged the importance of the ISG’s work, which it described as
21 “the only robust evidential basis on which a badger cull could take place”
22 (<http://www.publications.parliament.uk/pa/cm200708/cmselect/cmenvfru/130/130i.pdf>
23 f).

24

25 **2. Recent advances in knowledge**

1 2.1. Epidemiology of bTB in badgers

2 Bovine TB is a chronic infectious disease caused by the bacterium
3 *Mycobacterium bovis*. It affects a broad range of mammalian hosts including humans,
4 cattle, deer and wild carnivores such as badgers. Although the extent to which badgers
5 contribute to infection in cattle is still unclear, the results of the RBCT suggested they
6 accounted for around 50% in the experimental areas (Jenkins et al., 2008). The precise
7 routes of transmission amongst badgers and between badgers and cattle have yet to be
8 described. The distribution of lesions in badgers at *post mortem* examination and the
9 observation that *M. bovis* is most frequently isolated from sputum during live
10 sampling, suggest that the respiratory route may be most important for badger to
11 badger transmission (Clifton-Hadley et al., 1993; Corner, 2006). Onward transmission
12 to cattle may potentially occur through either direct contact with badgers themselves,
13 or with their excretory products. Incidence and transmission rates appear to be
14 relatively low in badgers and bTB apparently has little detectable impact on badger
15 population size or turnover (see Rogers et al., 1997, 2000). Infected badgers may live
16 for several years, during which time they may continue to breed (Delahay et al.,
17 2005), although individuals with evidence of continual excretion appear to exhibit
18 significantly higher levels of mortality (Wilkinson et al., 2000). Counter-intuitively,
19 recent analyses of a longitudinal study of badgers at Woodchester Park,
20 Gloucestershire, UK revealed a significant negative correlation between population
21 size and the detected incidence of excretion of *M. bovis* (Vicente et al., 2007). This
22 study showed that individual and group-level incidence risks were related to changes
23 in social group size and movement patterns of badgers amongst groups, highlighting
24 the profound importance of social structure in disease transmission dynamics.

25

1 2.2. *Epidemiological consequences of culling badgers*

2 Past studies from the UK and RoI provided compelling evidence that comprehensive,
3 localised badger culling operations reduced disease in cattle (see Clifton-Hadley et al.,
4 1995; Ó Máirtín et al., 1998; Eves, 1999). However, these studies did not incorporate
5 sufficient experimental controls or replication to provide conclusive scientific
6 evidence, and did not investigate the potential detrimental effects of culling in
7 adjoining areas. The RBCT took place between 1998 and 2005 in thirty 100 km²
8 treatment areas of high bTB incidence in cattle herds in west and south-west England.
9 The treatment areas were arranged into ten triplets, each of which contained an area
10 subjected to reactive culling (localised culling in response to a TB outbreak in cattle),
11 an area of proactive culling (widespread annual culling throughout the treatment area)
12 and a survey-only area, where no culling was carried out. This acted as an
13 experimental control against which the results of the other two treatments could be
14 measured (Independent Scientific Group, 2007).

15 The reactive culling treatment was stopped early by Ministers in November
16 2003 due to an observed 20% increase in the incidence of bTB in resident cattle herds
17 compared to survey-only areas (Donnelly et al., 2003). Despite debate over the
18 magnitude of the detrimental impact of reactive culling, and over the biological
19 plausibility and statistical treatment of the results (More et al., 2007), the ISG
20 concluded that reactive culling as carried out in the RBCT was, “unacceptable as a
21 policy option.” Proactive culling, on the other hand, demonstrated a significant
22 reduction (23%) in the incidence of cattle TB breakdowns inside culled areas after
23 approximately five years of culling (Independent Scientific Group, 2007; Donnelly et
24 al., 2007). This beneficial effect increased to 54% in the post-trial period (from one to
25 two years after the last proactive cull; Jenkins et al., 2008). However, this was

1 accompanied by a 25% increase in the incidence of bTB breakdowns in a 2 km wide
2 buffer zone around the proactive areas (Independent Scientific Group, 2007; Donnelly
3 et al., 2007), which subsequently disappeared in the post-trial period, 1-2 years after
4 culling ceased (Jenkins et al., 2008). Also, within the culled areas there was a
5 tendency for the incidence of herd breakdowns to increase with proximity to the
6 boundary, although these negative effects of culling diminished with successive
7 annual culls (Donnelly et al., 2007). Ongoing analyses in the post-trial period continue
8 to produce complex results. After three years since the end of culling, benefits inside
9 culled areas were no longer detectable. However, repeating this analysis using a
10 further six months of cattle testing data indicated that the beneficial effects observed
11 within trial areas in the first year post-trial had unexpectedly reappeared, with
12 confirmed breakdowns being 37% lower than survey-only areas (Jenkins et al., 2010).
13 Despite these complex outcomes, the experiment demonstrated that proactive badger
14 culling sustained for several years on a relatively large scale resulted in a positive
15 impact on herd breakdown incidence. However, the overall benefits in terms of the
16 number of breakdowns prevented were considered “modest”, and several years of
17 post-culling benefits would be required to offset the costs involved in carrying out the
18 culling (as conducted in the RBCT; Independent Scientific Group, 2007). Another
19 large-scale study in RoI compared the effects of two different culling strategies on the
20 control of bTB in four paired study areas (Griffin et al., 2005). The probability of a
21 cattle herd breakdown was significantly lower in areas where badgers were
22 proactively culled (removal areas) than in paired ‘reference areas’ where they were
23 only locally culled in response to a severe herd breakdown. Although the reference
24 areas did not represent a strict experimental control, the magnitude of the relative
25 beneficial effect of culling in the removal areas was compelling. In practice, very few

1 badgers were removed from the reference areas and there was no evidence that such
2 small-scale culling led to an increase in herd breakdowns as had been observed
3 following localised culling in the RBCT. This suggests that the negative effects
4 associated with culling on the UK mainland may not necessarily occur in Ireland,
5 where agricultural practices, landscape composition and badger density and ecology
6 may differ. This notion is supported by research from County Laois in RoI which
7 showed that badger removal following herd breakdowns was associated with a
8 beneficial impact on the time to future breakdowns for both index and surrounding
9 farms (Olea-Popelka et al., 2009).

10

11 *2.2.1. Unravelling the wider significance of badger sociality to disease control*

12 The temporary negative impacts of badger culling on herd breakdown rates observed
13 in the RBCT were attributed to disruption caused to otherwise stable badger
14 populations. There is a substantial body of evidence from the RBCT itself and other
15 studies in the UK and RoI that culling badgers may result in increased immigration
16 into culled areas, disruption of territoriality, increased ranging by individuals and
17 mixing of social groups, which may persist for many years (reviewed in Carter et al.,
18 2007). Such “social perturbation” may potentially lead to an increased risk of disease
19 transmission amongst badgers and between badgers and cattle. Culling during the
20 RBCT resulted in significant disruption of badger territories (Woodroffe et al., 2006a)
21 and was associated with an increase in the prevalence of infection in badgers
22 (Woodroffe et al., 2006b; Independent Scientific Group, 2007). Comparable
23 disruption of social structure was observed in previous studies of badger removal
24 operations in England and RoI (Cheeseman et al., 1993; O’Corry-Crowe et al., 1996;
25 Tuytens et al., 2000). In an intensively studied, undisturbed population, strong

1 associations were identified between badger movement patterns and the risks of bTB
2 infection (Rogers et al., 1998; Vicente et al., 2007).

3 The observed differences between the outcomes of badger culling in RoI and
4 mainland UK are intriguing. The absence of an increase in herd breakdowns in the
5 Irish Four Areas project (Griffin et al., 2005) may in part be due to its design, being
6 deliberately located in areas where natural barriers such as rivers, mountain ranges
7 and sea inlets are likely to have impeded the immigration of badgers from surrounding
8 areas. Another factor may be the lower density of badger populations in Ireland
9 compared to those in the bTB affected areas of Britain (Independent Scientific Group,
10 2007). Between 0.76 and 2.77 badgers were culled per km² in the proactive areas of
11 the RBCT, compared to 0.29 – 0.48 badgers per km² in the Four Areas project. At
12 medium to high densities, typical of south-west England and Wales, badgers tend to
13 reside in discrete social groups with well-defined territories and low rates of dispersal
14 (Kruuk and Parish, 1982; Woodroffe et al., 1993; Rogers et al., 1998). At low
15 densities however, badgers may adopt a more flexible social structure (Cheeseman et
16 al., 1993; Revilla and Palomares, 2002). Under these circumstances, it is possible that
17 lower density, associated reduced immigration pressure and the less marked spatial
18 structure may reduce the potential epidemiological consequences of culling. It
19 remains to be seen to what extent future developments in ‘trap-side’ diagnostics may
20 open the door to selective, and hence potentially less disruptive culling strategies,
21 perhaps also in combination with vaccination.

22 The effects of social perturbation present a significant challenge to the
23 management of infection risks from a reservoir in wildlife, and such problems are not
24 unique to badgers and bTB. There is also evidence that culling-induced social
25 perturbation may have hampered the control of rabies in red fox (*Vulpes vulpes*)

1 populations (Macdonald, 1995) and of Classical Swine Fever in wild boar (*Sus scrofa*;
2 Maillard and Fournier, 1995).

3

4 **3. Current research directions**

5 *3.1. Vaccination of badgers*

6 The vaccination of badgers and cattle has long been viewed as an attractive disease
7 control option. The basic aim of a badger vaccination strategy is to reduce the risk of
8 onward transmission of bTB from badgers to cattle. Inherent attractions of vaccination
9 as a disease management tool are that, unlike culling, it is not expected to disrupt
10 badger social behaviour and is unlikely to be opposed by conservationists, welfare
11 groups and the general public. However, the development of an effective vaccine,
12 with an appropriate strategy for its delivery, and its realisation as a commercially
13 available, licensed product involves considerable technical and regulatory challenges
14 (Blancou et al., 2009). Options for vaccinating badgers include capture and manual
15 delivery of the vaccine either directly into the oral cavity or by intra-muscular
16 injection, or oral delivery through deployment of bait without the need to capture
17 animals.

18 BCG (Bacille Calmette-Guerin) is presently the only candidate vaccine and
19 has been shown to be safe when administered parenterally to captive badgers
20 (Lesellier et al., 2006). A field study in the UK to evaluate the safety of intramuscular
21 delivery of BCG in badgers and to collect supporting data on vaccine immunogenicity
22 and efficacy was completed in November 2009. This study of approximately 90
23 contiguous badger social groups in south-west England began in 2006 and results are
24 anticipated by mid-2010. Badger social groups were allocated to either vaccination or
25 control treatments. Individuals captured in vaccinate groups were injected with 2-8 x

1 10⁶ colony forming units (cfu) of BCG. All captured badgers were uniquely marked,
2 physically examined and had a suite of clinical samples taken to determine disease
3 status and to detect the presence of *M. bovis* or BCG in clinical samples. The safety of
4 the vaccine was assessed by comparing vaccinated badgers with unvaccinated
5 controls in terms of body temperature following injection and local reactions at the
6 vaccination site on recapture. Samples were also taken for histological examination
7 from any vaccinated animals found dead in the study area.

8 Laboratory studies have been conducted in the UK and RoI on captive badgers
9 to determine the efficacy of BCG delivered via several routes. Evidence of a
10 protective effect, measured in terms of the immunological response and the severity of
11 pathology observed at *post-mortem* examination following experimental infection in
12 uninfected badgers, has been demonstrated (Corner et al., 2008; Lesellier et al., 2006,
13 2009). The results of the above field and laboratory studies formed the basis of an
14 application submitted to the Veterinary Medicines Directorate (the UK veterinary
15 medicines licensing body) in 2009 to obtain a Marketing Authorisation (MA) for the
16 intramuscular administration of BCG Danish 1331 to wild badgers. This was granted
17 in March 2010.

18 The UK Government began using the licensed injectable vaccine in the Badger
19 Vaccine Deployment Project in July 2010 (BVDP;
20 <http://www.defra.gov.uk/fera/bvdp>). This is a six-year project to deploy vaccine to
21 wild badgers in a bTB-affected area in England. Badgers are captured in cage traps
22 and vaccinated in the field by government staff on up to 100 km² of predominantly
23 cattle land. Unlike other components of the vaccine programme this is neither a
24 research project nor a regulatory study, but rather aims to provide training for lay-
25 vaccinators, assess the viability of field application of an injectable badger vaccine,

1 and build industry confidence in the principle and practicalities of wildlife
2 vaccination. It is intended that the project will provide valuable information on the
3 true costs and practicalities of large-scale vaccine deployment. It will also provide an
4 opportunity to engage the farming community, and potentially, to begin to make a
5 positive impact on a badly affected area before an oral vaccine formulation is
6 available. A social science study is also being conducted with participating and non-
7 participating farmers, to establish levels of farmer confidence in the use of vaccination
8 before, during and after vaccine deployment.

9 It is generally recognised that delivery of vaccine in oral baits holds the best
10 long-term prospect for deployment to badgers over a wide area (see Delahay et al.,
11 2003). The large-scale eradication of sylvatic rabies in Europe through the vaccination
12 of red foxes using oral baits (Brochier et al., 1991) represents an important precedent
13 for the wide-scale vaccination of badgers in the UK and RoI. The success of such an
14 approach will depend on how many badgers consume the baits and the effectiveness
15 of the vaccine. Collaborative research and development studies are currently
16 underway in both countries towards a common aim of identifying how this might be
17 achieved in practice. Work has already taken place on bait delivery systems for
18 badgers (e.g. Delahay et al., 2000) and on identifying the most palatable baits. Current
19 research is aimed at identifying the most appropriate bait formulation to ensure that
20 BCG remains viable for prolonged periods in the bait, is not incapacitated by acidic
21 conditions in the stomach, but can be delivered where it is most likely to induce
22 protective immunity to *M. bovis*. A recent study in New Zealand achieved an
23 estimated efficacy of 95% in wild brush-tail possums (*Trichosurus vulpecula*) using a
24 lipid-formulated oral vaccine containing 10^7 cfu BCG delivered to the rear of the oral
25 cavity (Tomkins et al., 2009). In light of these promising results, a large field trial

1 began in 2009 in RoI, designed to measure the protection generated by BCG
2 vaccination in wild badgers, and to estimate vaccine efficacy by comparing the
3 prevalence of *M. bovis* infection in vaccinated and non-vaccinated badgers (Corner et
4 al., 2009). Badgers are trapped in an area comprised of three zones, in which 100%,
5 50%, or none of the captured badgers are vaccinated using the lipid formulation
6 delivered directly into the pharynx under general anaesthetic. These proportions were
7 selected such that effects on vaccine efficacy due to changes in the force of infection
8 as a result of vaccination could be estimated (Corner et al., 2009). Badgers will be
9 vaccinated annually for three years, at which point the area will be depopulated and
10 all captured badgers submitted for *post mortem* examination, histology and bacterial
11 culture.

12 Field studies to determine the optimum deployment method for an oral vaccine
13 bait began in England in May 2010. The relative uptake rates of the most promising
14 candidate baits, devoid of vaccine, will be assessed at different times of year. The
15 study will also investigate variations in bait uptake rates relative to deployment of bait
16 above and below ground (i.e. down sett entrances), and the duration of bait provision.
17 The aim is to identify the most cost-effective and practical strategy for maximising
18 bait uptake by badgers. Alongside this, studies will be conducted on the efficacy of
19 the oral vaccine under experimental, controlled conditions. The results of this work
20 are expected by 2012 at which point it will be necessary to conduct regulatory studies
21 to demonstrate safety of the final product to both captive and wild animals. The
22 earliest anticipated date for a licensed oral vaccine is 2015. In addition to the science,
23 there are a number of key policy, legal, commercial, regulatory and manufacturing
24 issues surrounding the implementation of a vaccine against bTB.

25

1 3.2. Farm biosecurity

2 The principal routes of *M. bovis* transmission between badgers and cattle are unclear.
3 Badgers forage for earthworms on grassland and their preference for grazed pasture
4 creates opportunities for cattle to come into direct contact with them and their
5 excretory products (Muirhead et al. 1974; MAFF 1979; Wilesmith et al. 1982). Direct
6 contact between live badgers and cattle on pasture has been documented (Böhm et al.,
7 2009), and there are anecdotal reports of cattle investigating badger carcasses. Most
8 research on potential transmission risks has in the past concentrated on the
9 contamination of cattle pasture with badger faeces and urine, particularly at latrines
10 (Benham, 1985; MAFF, 1979; Cheeseman and Mallinson, 1981; Benham and Broom,
11 1989; Hutchings and Harris, 1997; 1999). However, evidence suggests that badger
12 visits to farm buildings might also give rise to opportunities for transmission (MAFF,
13 1979; 1981; 1987; Cheeseman and Mallinson, 1981; Benham, 1985; Kruuk and
14 Parish, 1985; Shepherdson et al., 1990; Brown, 1993; Sleeman and Mulcahy, 1993).
15 Studies using intensive nocturnal observations, radio tracking, video and camera
16 surveillance revealed that badger visits to buildings on some farms occurred on over
17 50% of nights investigated (Garnett et al., 2002; 2003; Tolhurst, 2006; Ward et al.,
18 2008). Visiting badgers used a variety of resources including feed stores, silage
19 clamps and cattle housing. Badgers, including known infected individuals, were
20 recorded defecating and urinating in buildings, sometimes directly onto feed and
21 regularly came within 2m of housed cattle (Garnett et al., 2002; Roper et al., 2003,
22 Tolhurst, 2006). These studies highlighted the potential for this phenomenon to be an
23 important risk factor for disease transmission on some farms, although the
24 contribution of such behaviour to cattle herd breakdown rates has not been quantified.
25 Nevertheless, it is clear that the development of practical means of managing badger-

1 cattle interactions is likely to be more achievable in and around farm buildings than
2 on pasture.

3 A recent field experiment employing a factorial design investigated the effects
4 of a series of badger exclusion measures on 32 farms in south-west England
5 (Unpublished Defra report). Badger-proofed gates, feed stores and doors, and electric
6 fences, were deployed on cattle feed stores, cattle housing and silage clamps (all of
7 which were known to be visited by badgers) and monitored using remote camera
8 surveillance. The results yielded unequivocal evidence that when exclusion measures
9 were employed and adequately maintained they provided 100% protection of feed
10 stores and cattle housing from badger incursions. However, levels of farmer
11 compliance varied widely, suggesting the existence of cultural/behavioural barriers in
12 the farming community to changing established working practices.

13 The costs of badger exclusion are likely to vary widely, depending on the
14 characteristics of the particular farm in question. As the contribution of such measures
15 to a reduced risk of experiencing a cattle herd breakdown is unknown, their cost-
16 effectiveness cannot be quantified or communicated to farmers at present. Therefore
17 presenting a convincing argument for the value of investing time and money in
18 improved biosecurity measures is a significant challenge. Given the potential disease
19 risks associated with badgers visiting farm buildings, encouraging farmers to take
20 steps to reduce this risk has obvious value. In an attempt to address this, the Welsh
21 Assembly Government established a biosecurity Intensive Treatment Area (ITA) in a
22 high incidence area of west Wales (G. Enticott, 2008) with the aim of raising
23 awareness, understanding, and adoption of biosecurity measures. Local veterinarians
24 visited farms, assessed the existing biosecurity arrangements and provided advice on

1 practical improvements. Farmers appeared to respond positively and improvements in
2 biosecurity were observed (G. Enticott, 2008).

3

4 **4. Translating science into policy**

5 Bovine TB continues to have a devastating impact on the farming industry in some
6 parts of the UK and RoI, as well as on the public purse. However, owing to the
7 chronic nature and complexity of the disease, translating our scientific understanding
8 into effective policy is not a straightforward task. It is clear that bTB risks to cattle are
9 multi-faceted, requiring an integrated approach including both cattle and wildlife-
10 based controls. The compulsory test and slaughter of positive (reactor) cattle and
11 associated movement restrictions remain the principal method of controlling bTB in
12 cattle herds in the UK and RoI. While vaccination of cattle is seen as a potential
13 important longer-term policy option in the UK, the eradication of bTB from cattle in
14 high-incidence areas of both countries is unlikely to be achieved without addressing
15 potential re-infection from badgers. The three main ways in which this may be
16 addressed are culling, vaccination and bio-security measures to prevent or at least
17 reduce contact between badgers and cattle. The complexity of this problem is
18 highlighted by the different management approaches currently being adopted by the
19 respective authorities of the UK where bTB is a problem (England, Wales and
20 Northern Ireland), and in and RoI. In light of a range of considerations including the
21 ISG's conclusions from the RBCT, the previous UK Government decided that
22 licences would not be issued to farmers to cull badgers for bTB in England, and
23 increased investment in research into vaccination for badgers, as well as cattle. In RoI
24 routine reactive culling continues to form part of government policy, supported by
25 evidence from field studies, in particular the Four Areas project. Reactive culling has

1 been conducted throughout RoI since the early 1990s where it is viewed as an interim
2 wildlife control strategy. Badgers are removed under licence within a 1-2 km radius
3 around a farm that has suffered a herd breakdown and where badgers are suspected to
4 be the source of infection. The Welsh Assembly Government (WAG; the devolved
5 government of Wales) announced in 2009 that in addition to a range of bTB control
6 measures nationally, proactive badger culling would be conducted alongside more
7 stringent cattle controls within an Intensive Action Pilot Area (IAPA) in Wales. In
8 Northern Ireland (NI), limited badger removal remains a potential option, in the
9 context of investigating badger-related risk factors on farms with and without bTB
10 infection. The Department of Agriculture and Rural Development in NI recently
11 funded a national survey, establishing that there had been little change in badger
12 distribution and population size in NI since an initial baseline survey in the early
13 1990s (Reid et al., 2008).

14 The vaccination of badgers is seen as an important potential policy option for
15 reducing the risk of bTB in cattle throughout the UK and RoI. This is reflected in the
16 significant portions of the respective bTB research budgets that have been allocated to
17 these approaches. Within Defra, the total investment in vaccine development for
18 badgers and cattle exceeded £30 million from 1998 up until April 2010. The UK
19 general election in May 2010 resulted in a change in Government. At the time of
20 writing, the new Government is reviewing options for wildlife TB research and
21 management in the light of background economic pressures and their own policy
22 position. Early outcomes of this process include a reduction in the scope of the BVDP
23 from six target areas to one, and renewed consideration of culling as well as
24 vaccination options.

25

1 5. Conclusion

2 Bovine TB is the most serious endemic disease currently facing livestock in the UK
3 and the RoI, and its cost to the farming industry and the taxpayer is unsustainable. It is
4 widely recognised that a sustainable solution can only be reached through a multi-
5 faceted approach using a variety of available tools, targeting both cattle and wildlife.
6 Such an approach is likely to include continued improvements in cattle testing,
7 enhanced farm biosecurity and the deployment of cattle and badger vaccines as they
8 become available. In the meantime badger culling continues in the RoI, is planned to
9 start in a targeted area of Wales, is still under consideration in Northern Ireland, and is
10 under review in England by the new UK Government.

11 Recent research in the UK and RoI has significantly increased our knowledge
12 of the role of the badger in the dynamics of bTB infection in cattle, and in the
13 outcome of strategies for intervention. It has become clear that aspects of badger
14 ecology may significantly influence the outcomes of culling. How differences in the
15 prevailing density and social structure of badger populations might influence the
16 outcome of culling operations remains unknown. Other crucial gaps in our knowledge
17 include the precise route of transmission of *M. bovis* between badgers and cattle, and
18 the extent to which badgers with advanced disease may exhibit behavioural traits that
19 increase the likelihood of onward transmission. Nevertheless, strategies to reduce
20 disease transmission among badgers and cattle will have to be developed in the
21 absence of complete knowledge.

22 Practical steps to improve biosecurity have been shown to be sufficient to
23 exclude badgers from farm buildings. However, the cost of such activities in terms of
24 both money and time is a deterrent to farmers. In the absence of proof that improving
25 biosecurity reduces the risks of herd breakdowns, convincing farmers of the value of

1 implementing such measures remains a significant challenge of communication for
2 government and the veterinary profession.

3 Vaccination of cattle and badgers is still considered to have the potential to
4 contribute significantly to a long-term solution to the bTB problem. A wide-ranging
5 research program is underway in the UK and RoI, aimed at developing vaccine
6 products and deployment protocols for the wide-scale vaccination of badger
7 populations. In parallel with this research, badgers are being vaccinated in a badly
8 affected area of England from 2010, and it is intended that the practical lessons learnt
9 will inform future vaccination policy for when an oral vaccine bait becomes available.

10 It is clear that management of bTB in badgers and cattle is a considerable
11 veterinary and ecological challenge. Management of the disease in cattle by reducing
12 badger population densities through culling has mixed, unpredictable and in some
13 cases undesirable outcomes. The ISG's findings in particular highlight the need to
14 consider the ecological complexities of wild animal populations when taking
15 decisions on disease management. Indeed, owing to the complex ecology of not only
16 badgers, but also the characteristics of *M. bovis*, the effectiveness of bTB management
17 may continue to be constrained by an imperfect knowledge of the wildlife host or host
18 community. Going forward, management of bTB will require input from
19 veterinarians, epidemiologists and ecologists, mathematical modellers, economists
20 and others. The current efforts to develop cost-effective vaccine deployment strategies
21 for badgers are promising examples of such a multi-disciplinary approach.

22

23 **Acknowledgements**

24 The authors thank the Department for Environment Food and Rural Affairs for
25 funding much of the work reviewed in this paper, Mark Chambers for helpful

1 comments on an earlier draft, Carol Christie for help in preparing the final manuscript,
2 and two anonymous referees for their comments.

3

4 **Conflict of Interest Statement**

5 The authors have not declared any conflict of interest.

6

7 **References**

- 8 Badger Stakeholder Group, 2008. Report of the DARD badger stakeholder group.
9 <http://www.dardni.gov.uk/badger-stakeholder-group-report.pdf>
- 10 Benham, P. F. J., 1985. A study of cattle and badger behaviour and farm husbandry
11 practices relevant to the transmission of bovine tuberculosis (*Mycobacterium*
12 *bovis*). Report to MAFF Chief Scientists's Group (1982-1985).
- 13 Benham, P. F. J., Broom, D. M., 1989. Interactions between cattle and badgers at
14 pasture with reference to bovine tuberculosis transmission. Br. Vet. J. 145, 226-
15 241.
- 16 Blancou, J., Artois, M., Gilot-Fromont, E., Kaden, V., Rossi, S., Smith, G. C.,
17 Hutchings, M. R., Chambers, M. A., Houghton, S., Delahay, R. J., 2009. Options
18 for the control of disease: targeting the infectious or parasitic agent. In
19 Management of Disease in Wild Mammals. Delahay, R. J., Smith, G. C.,
20 Hutchings, M. R. (eds). Springer Tokyo. pp97-120.
- 21 Böhm, M., Hutchings, M. R., White, P. C. L., 2009. Contact networks in a wildlife-
22 livestock host community: identifying high-risk individuals in the transmission of
23 bovine TB among badgers and cattle. PLoS ONE 4(4): e5016.
24 doi:10.1371/journal.pone.0005016.
- 25 Brochier, B., Kieny, M. P., Costy, F., Coppens, P., Bauduin, B., Lecocq, J. P.,
26 Languet, B., Chappuis, G., Desmettre, P., Afiademanyo, K., Libois, R., Pastoret,
27 P.-P., 1991. Large-scale eradication of rabies using recombinant vaccinia-rabies
28 vaccine. Nature. 354, 520–522.
- 29 Brown, J. A., 1993. Transmission of bovine tuberculosis (*Mycobacterium bovis*) from
30 badgers (*Meles meles*) to cattle. PhD. Thesis, University of Bristol.
- 31 Carter, S. P., Delahay, R. J., Smith, G. C., Macdonald, D. W., Riordan, P.,
32 Etherington, T. R., Pimley, E. R., Walker, N. J., Cheeseman, C. L., 2007. Culling-
33 induced social perturbation in Eurasian badgers *Meles meles* and the management
34 of TB in cattle: an analysis of a critical problem in applied ecology. Proc. R. Soc.
35 B. 274, 2769-2777.
- 36 Cheeseman, C. L., Mallinson, P. J., 1981. Behaviour of badgers (*Meles meles*)
37 infected with bovine tuberculosis. J. Zool. 194, 284-289.
- 38 Cheeseman, C. L., Mallinson, P. J., Ryan, J., Wilesmith, J. W., 1993. Recolonisation
39 by badgers in Gloucestershire. In Hayden, T. J. (ed.). The Badger, pp. 78-93.
40 Royal Irish Academy, Dublin.
- 41 Clifton-Hadley, R. S., Wilesmith, J. W., Richards, M. S., Upton, P., Johnston, S.,
42 1995. The occurrence of *Mycobacterium bovis* infection in and around an area

- 1 subject to extensive badger (*Meles meles*) control. Epidemiol. Infect. 114, 179-
2 193.
- 3 Clifton-Hadley, R. S., Wilesmith, J. W., Stuart, F. A., 1993. *Mycobacterium bovis* in
4 the European badger (*Meles meles*): Epidemiological findings in tuberculous
5 badgers from a naturally infected population. Epidemiol. Infect. 111, 9-19.
- 6 Corner, L. A. L., 2006. The role of wild animal populations in the epidemiology of
7 tuberculosis in domestic animals: How to assess the risk. Vet. Microbiol. 112,
8 303-312.
- 9 Corner, L. A. L., Costello, E., Lesellier, S., O'Meara, D., Gormley, E., 2008.
10 Vaccination of European badgers (*Meles meles*) with BCG by the subcutaneous
11 and mucosal routes induces protective immunity against endobronchial challenge
12 with *Mycobacterium bovis*. Tuberculosis. 88, 601-609.
- 13 Corner, L. A. L., Murphy, D., Costello, and Gormley, E., 2009 Tuberculosis in
14 European badgers (*Meles meles*) and the control of infection with Bacille
15 Calmette-Guerin vaccination. J. Wild. Dis. 45, 1042-1047.
- 16 Delahay, R. J., Brown, J. A., Mallinson, P. J., Spyvee, P. D., Handoll, D., Rogers, L.
17 M., Cheeseman, C. L., 2000. The use of marked bait in studies of the territorial
18 organisation of the European badger (*Meles meles*). Mamm. Rev. 30(2), 73-87.
- 19 Delahay, R. J., Wilson, G. J., Smith, G. C., Cheeseman, C. L., 2003. Vaccinating
20 badgers (*Meles meles*) against *Mycobacterium bovis*: The ecological
21 considerations. Vet. J. 166, 43-51.
- 22 Delahay, R. J., Smith, G. C., Ward, A. I., Cheeseman, C. L., 2005. Options for the
23 Management of Bovine Tuberculosis Transmission from Badgers (*Meles meles*) to
24 cattle: Evidence from a long-term study. Mamm. Study. 30, S73-S81.
- 25 Donnelly, C. A., Woodroffe, R., Cox, D. R., Bourne, J., Gettinby, G., Le Fevre, A.
26 M., McInerney, J. P., Morrison, I., 2003. Impact of localized badger culling on
27 tuberculosis incidence in British cattle. Nature. 426, 834-837.
- 28 Donnelly, C. A., Wei, G., Johnston, W. T., Cox, D. R., Woodroffe, R., Bourne, F. J.,
29 Cheeseman, C. L., Clifton-Hadley, R. S., Gettinby, G., Gilks, P., Jenkins, H. E.,
30 Le Fevre, A. M., McInerney, J. P., Morrison, W. I., 2007. Impacts of widespread
31 badger culling on cattle tuberculosis: concluding analyses from a large-scale field
32 trial. Int. J. Infect. Dis. 11, 300-308.
- 33 Enticott, G., 2008. Evaluation of the South West Wales Biosecurity Intensive
34 Treatment Area. Report to the Welsh Assembly Government.
- 35 Eves, J. A., 1999. Impact of badger removal on bovine tuberculosis in east County
36 Offaly. Irish Vet. J. 52, 199-203.
- 37 Garnett, B. T., Delahay, R. J., Roper, T. J., 2002. Use of cattle farm resources by
38 badgers (*Meles meles*) and risk of bovine tuberculosis (*Mycobacterium bovis*)
39 transmission to cattle. Proc. Roy. Soc. B. 269, 1487-1491.
- 40 Garnett, B. T., Roper, T. J., Delahay, R. J., 2003. Use of cattle troughs by badgers
41 (*Meles meles*) a potential route for the transmission of bovine tuberculosis
42 (*Mycobacterium bovis*) to cattle. Appl. Anim. Behav. Sci. 80, 1-8.
- 43 Griffin, J. M., Williams, D. H., Kelly, G. E., Clegg, T. A., O'Boyle, I., Collins, J. D.,
44 More, S. J., 2005. The impact of badger removal on the control of tuberculosis in
45 cattle herds in Ireland. Prev. Vet. Med. 67(4), 237-266.
- 46 Hutchings, M. R., Harris, S., 1997. Effects of farm management practices on cattle
47 behaviour and the potential for transmission of bovine tuberculosis from badgers
48 to cattle. Vet. J. 153, 149-162.
- 49 Hutchings, M. R., Harris, S., 1999. Quantifying the risks of TB infection to cattle
50 posed by badger excreta. Epidemiol. Infect. 122, 167-174.

- 1 Independent Scientific Group., 2007. Bovine TB: The Scientific Evidence, A Science
2 Base for a Sustainable Policy to Control TB in Cattle, An Epidemiological
3 Investigation into Bovine Tuberculosis. Final Report of the Independent Scientific
4 Group on Cattle TB. London: Department for Environment, Food & Rural Affairs.
- 5 Jenkins, H. E., Woodroffe, R., Donnelly, C. A., 2008. The effects of annual
6 widespread badger culls on cattle tuberculosis following the cessation of culling.
7 Int. J. Infect. Dis. 12, 457-465.
- 8 Jenkins, H. E., Woodroffe R., Donnelly, C. A. (2010) The Duration of the Effects of
9 Repeated Widespread Badger Culling on Cattle Tuberculosis Following the
10 Cessation of Culling. PLoS ONE 5(2): e9090. doi:10.1371/journal.pone.0009090.
- 11 Krebs, J. R., 1997. Bovine tuberculosis in cattle and badgers. MAFF, London.
- 12 Kruuk, H., Parish, T., 1982. Factors affecting population density, group size and
13 territory size of the European badger, *Meles meles*. J. Zool. 196, 31-39.
- 14 Kruuk, H., Parish, T., 1985. Food, food availability and weight of badgers (*Meles*
15 *meles*) in relation to agricultural changes. J. Appl. Ecol. 22, 705-715.
- 16 Lesellier, S., Palmer, S., Dalley, D. J., Dave, D., Johnson, L., Hewinson, R. G.,
17 Chambers, M. A., 2006. The safety and immunogenicity of Bacillus Calmette-
18 Guerin (BCG) vaccine in European badgers (*Meles meles*). Vet. Immunol.
19 Immunop. 112, 24-37.
- 20 Lesellier, S., Corner, L., Costello, E., Lyashchenko, K., Greenwald, R., Esfandiari, J.,
21 Singh, M., Hewinson, R. G., Chambers, M., Gormley, E., 2009. Immunological
22 responses and protective immunity in BCG vaccinated badgers following
23 endobronchial infection with *Mycobacterium bovis*. Vaccine. 27, 402-409.
- 24 Maillard, D., Fournier P., 1995. Effect of shooting with hounds on size of resting
25 range of wild boar (*Sus scrofa L.*) groups in mediterranean habitat. IBEX JME, 3,
26 102-107.
- 27 MAFF., 1979. Bovine tuberculosis in badgers. Third report by the Ministry of
28 Agriculture, Fisheries and Food. MAFF, London.
- 29 MAFF., 1981. Bovine tuberculosis in badgers. Fifth report by the Ministry of
30 Agriculture, Fisheries and Food. MAFF, London.
- 31 MAFF., 1987. Bovine tuberculosis in badgers. Eleventh report by the Ministry of
32 Agriculture, Fisheries and Food. MAFF, London.
- 33 Macdonald, D. W., 1995. Wildlife rabies: the implications for Britain. Unresolved
34 questions for the control of wildlife rabies: social perturbation and interspecific
35 interactions. In: Beynon, P.H., Ednay, A.T.B. (Eds) Rabies in a changing world.
36 British Small Animal Veterinary Association, Cheltenham, pp. 33-48,
- 37 More, S. J., Clegg, T. A., McGrath, G. Collins, J. D., Corner, L. A., Gormley, E.,
38 2007. Does reactive badger culling lead to an increase in tuberculosis in cattle?
39 Vet. Rec. 161, 208-209.
- 40 Muirhead, R. H., Gallagher, J., Burn, K. J., 1974. Tuberculosis in wild badgers in
41 Gloucestershire: Epidemiology. Vet. Rec. 95, 552-555.
- 42 O'Corry-Crowe, G., Hammond, R., Eves, J., Hayden, T. J., 1996. The effect of
43 reduction in badger density on the spatial organisation and activity of badgers
44 *Meles meles L.* in relation to farms in central Ireland. Biol. Environ. 96B, 147-
45 158.
- 46 Olea-Popelka, F. J., Fitzgerald, P., White, P., McGrath, G., Collins, J. D., O'Keeffe,
47 J., Kelton, D. F., Berke, O., More, S., Martin, S. W., 2009. Targeted badger
48 removal and the subsequent risk of bovine tuberculosis in cattle herds in county
49 Laois, Ireland. Prev. Vet. Med. 88, 178-184.

- 1 Ó Máirtín, D. O., Williams, D. H., Griffin, J. M., Dolan, L. A., Eves, J. A., 1998. The
2 effect of a badger removal programme on the incidence of tuberculosis in an Irish
3 cattle population. *Prev. Vet. Med.* 34, 47-56.
- 4 Reid, N., Etherington, T. R., Wilson, G. J., McDonald, R. A. & Montgomery, W. I.
5 (2008) *Badger survey of Northern Ireland 2007/08*. Report to the Department of
6 Agriculture & Rural Development (DARD), Northern Ireland, UK.
- 7 Revilla, E., Palomares, F., 2002. Spatial organization, group living and ecological
8 correlates in low-density populations of Eurasian badgers, *Meles meles*.
9 *J. Anim. Ecol.* 71, 497-512.
- 10 Rogers, L. M., Cheeseman, C. L., Mallinson, P. J., Clifton-Hadley, R., 1997. The
11 demography of a high density badger (*Meles meles*) population in the west of
12 England. *J. Zool.* 242, 705-728.
- 13 Rogers, L. M., Delahay, R. J., Cheeseman, C. L., Langton, S., Smith, G. C., Clifton-
14 Hadley, R., 1998. Movement of badgers (*Meles meles*) in a high density
15 population: Individual, population and disease effects. *Proc. Roy. Soc. B.* 265,
16 1269-1276.
- 17 Rogers, L. M., Delahay, R. J., Hounscome, T. D., Cheeseman, C. L., 2000. Changes in
18 badger, *Meles meles*, social organisation in response to increasing population
19 density at Woodchester Park, south-west England. Pp. 267-279 in Griffiths, H. I.
20 (ed.) *Mustelids in a modern world. Management and conservation aspects of small*
21 *carnivore: human interactions*. Backhuys Publishers, Netherlands.
- 22 Roper, T. J., Garnett, B. T., Delahay, R. J., 2003. Visits to farm buildings and cattle
23 troughs by badgers (*Meles meles*): a potential route for transmission of bovine
24 tuberculosis (*Mycobacterium bovis*) between badgers and cattle. *Cattle Practice*.
25 11, 9-12.
- 26 Shepherdson, D. J., Roper, T. J., Lüps, P., 1990. Diet, food availability and foraging
27 behaviour of badgers (*Meles meles* L) in southern England. *Mamm. Biol.* 55, 81-
28 93.
- 29 Sleeman, D. P., Mulcahy, M. F., 1993. Behaviour of Irish badgers in relation to
30 bovine tuberculosis. Pp 154-165 in Hayden, T. J. (ed.) *The badger*. Royal Irish
31 Academy, Dublin.
- 32 Tolhurst B. A., 2006. Behaviour of badgers (*Meles meles*) in farm buildings, in
33 relation to the transmission of bovine tuberculosis (*Mycobacterium bovis*) between
34 badgers and cattle. Unpublished PhD Thesis. University of Sussex
- 35 Tompkins, D. M., Ramsey, D. S. L., Cross, M. L., Aldwell, F. E., de Lisle, G. W.,
36 Buddle, B. M., 2009. Oral vaccination reduces the incidence of tuberculosis in
37 free-living brushtail possums. *Proc. Roy. Soc.* 276, 2987-2995
- 38 Tuytens, F. A. M., Delahay, R. J., Macdonald, D. W., Cheeseman, C. L., Long, B.,
39 Donnelly, C., 2000. Spatial perturbation caused by a badger (*Meles meles*) culling
40 operation: implications for the function of territoriality and the control of bovine
41 tuberculosis (*Mycobacterium bovis*). *J. Anim. Ecol.* 69(5), 815-828.
- 42 Vicente, J., Delahay, R. J., Walker, N., Cheeseman, C. L., 2007. Social organization
43 and movement influence the incidence of bovine tuberculosis in an undisturbed
44 high density badger *Meles meles* population. *J. Anim. Ecol.* 76, 348-360.
- 45 Ward, A. I., Tolhurst, B. A., Walker, N. J., Roper, T. J., Delahay R. J., 2008. A survey
46 of badger access to farm buildings and facilities in relation to contact with cattle.
47 *Vet. Rec.* 163, 107-111.
- 48 Wilesmith, J. W., Little, T. W. A., Thompson, H. V., Swan, C., 1982. Bovine
49 tuberculosis in domestic and wild mammals in an area of Dorset. 1. Tuberculosis
50 in cattle. *J. Hyg. Cambridge.* 89, 195-210.

- 1 Wilkinson, D., Smith, G. C., Delahay, R. J., Rogers, L. M., Cheeseman, C. L.,
2 Clifton-Hadley, R. S., 2000. The effects of bovine tuberculosis (*Mycobacterium*
3 *bovis*) on mortality in a badger (*Meles meles*) population in England. *J. Zool.* 250,
4 389-395.
- 5 Woodroffe R., Macdonald D. W., da Silva J., 1993. Dispersal and philopatry in the
6 European badger (*Meles meles*). *J. Zool.* 237, 227-239.
- 7 Woodroffe, R., Donnelly, C. A., Cox, D. R., Bourne, J. F., Cheeseman, C. L.,
8 Delahay, R. J., Gettinby, G., McInerney, J. P., Morrison, W. I., 2006a. Effects of
9 culling on badger *Meles meles* spatial organization: implications for the control of
10 bovine tuberculosis. *J. Appl. Ecol.* 42, 852-862.
- 11 Woodroffe, R., Donnelly, C. A., Jenkins, H. E., Johnston, W. T., Cox, D. R., Bourne,
12 F. J., Cheeseman, C. L., Delahay, R. J., Clifton-Hadley, R. S., Gettinby, G., Gilks,
13 P., Hewinson, R. G., McInerney, J. P., Morrison, W. I., 2006b. Culling and cattle
14 controls influence tuberculosis risk for badgers. *P. Natl. Acad. Sci. USA.* 103,
15 14713-14717.
- 16 Zuckerman, O. M., 1980. Badgers, cattle and tuberculosis. HMSO, London.
17