Eur J Wildl Res (2015) 61:263–269
DOI 10.1007/s10344-014-0896-y

ORIGINAL PAPER

Exposure of nontarget wildlife to candidate TB vaccine baits deployed for European badgers

Andrew Robertson · Mark A. Chambers · Richard J. Delahay · Robbie A. McDonald · Kate L. Palphramand · Fiona Rogers · Stephen P. Carter

Received: 3 September 2014 / Revised: 20 December 2014 / Accepted: 22 December 2014 / Published online: 14 January 2015

Abstract In the UK and Republic of Ireland, the European badger *Meles meles* is considered a maintenance host for bTB and is involved in transmission of infection to cattle. A badger vaccine delivered in an oral bait is currently under development as part of an ongoing effort to reduce levels of disease in the badger population. An oral vaccine would likely be deployed in close vicinity to badger burrows (setts), such that bait will most likely be taken by the target species. However, a range of nontarget species may also occur close to badger setts, and some may potentially interfere with or consume baits. In this study, we used surveillance cameras to record the presence of nontarget species at 16 badger setts involved in a bait deployment study in southwest England. We recorded significant levels of nontarget species activity close to badger setts. The most commonly observed species were small rodents, which were observed at all setts, and in some cases accounted for >90 % of nontarget species observations. A total of 11 other nontarget species were also observed, indicating that a broad range of species may potentially come into contact with vaccine baits deployed at badger setts. Although the majority of these species were not observed interacting directly with baits, small rodents and squirrels were observed eating baits in a number of instances. In addition, monitoring of bait disappearance at 24 setts indicated that small rodents may take >30 % of bait deployed at some setts. The implications for the deployment of an oral vaccine for badgers are discussed.

Keywords Badger · Bait uptake · Bovine tuberculosis · Nontarget · Oral vaccination · TB · BCG

Communicated by M. Artois

A. Robertson (✉) · R. A. McDonald
Environment and Sustainability Institute, University of Exeter, Penryn, Cornwall TR10 9EZ, UK
e-mail: a.robertson@exeter.ac.uk

A. Robertson · R. J. Delahay · K. L. Palphramand · F. Rogers · S. P. Carter
National Wildlife Management Centre, Animal and Plant Health Agency, Woodchester Park, Gloucestershire GL10 3UJ, UK

M. A. Chambers
Department of Bacteriology, Animal and Plant Health Agency, WeybridgeWoodham Lane, New Haw KT15 3NB, UK

M. A. Chambers
School of Veterinary Medicine, University of Surrey, Guildford, Surrey GU2 7XH, UK

Introduction

Bovine tuberculosis (bTB), caused by *Mycobacterium bovis*, is a globally important disease, infecting both livestock and humans (Palmer et al. 2012). *M. bovis* can also infect a diverse range of wild mammals, which complicates disease control in cattle in several countries where wild species can act as disease reservoirs and potential sources of infection (Nol et al. 2008; Beltrán-Beck et al. 2012; Palmer et al. 2012). In the United Kingdom (UK) and Republic of Ireland (ROI), the European badger *Meles meles* is considered a maintenance host for bTB and is involved in transmission of infection to cattle (Krebs 1997). Culling badger populations in Ireland has been associated with reductions in risks of disease incidence in cattle (Griffin et al. 2005). However, in England, culling badgers has had both positive and negative impacts on the incidence of disease in cattle (Clifton-Hadley et al. 1995; Donnelly et al. 2006), and there is significant public opposition to large-scale badger culling (White and Whiting 2000).

Vaccination of wildlife hosts is a potential alternative or complement to culling for managing bTB in wild animal populations (Cross et al. 2007). A suitable vaccine currently exists, in the form of Bacillus Calmette–Guérin (BCG), a live attenuated form of *M. bovis*. Vaccination with BCG has been instrumental in reducing TB (principally caused by the closely related *Mycobacterium tuberculosis*) in human populations and has proven to be safe and efficacious in several other mammals, including badgers (Murphy et al. 2008; Lesellier et al. 2011). Administration of BCG vaccine to badgers by injection has been shown to reduce disease severity and progression (Lesellier et al. 2011), as well as reducing risks of bTB infection among vaccinated and unvaccinated wild badgers (Chambers et al. 2011; Carter et al. 2012).

Currently, BCG is only licensed for administration to wild badgers by intramuscular injection which is labor-intensive and requires trained and licensed personnel (Brown et al. 2013). An alternative and potentially cheaper method to achieve broad vaccine coverage would be to deploy the vaccine in a palatable bait (Buddle et al. 2011; Robinson et al. 2012). This approach has proven highly effective at reducing sylvatic rabies in wild mammals in North America and Europe (Cross et al. 2007) and is currently being trialled for vaccinating wild boar *Sus scrofa* and brushtail possums *Trichosurus vulpecula* against bTB (Beltrán-Beck et al. 2012; Tompkins et al. 2013). BCG confers a degree of protection in badgers when orally administered (Corner et al. 2010), and an oral badger vaccine is currently under development (http://www.defra.gov.uk/ahvla-en/science/bovine-tb/). However, the development of an efficacious oral vaccine is only part of the solution as it is also necessary to develop an effective delivery system. This work is also currently underway, but there are some specific challenges associated with delivering an oral vaccine to free-living wildlife (Chambers et al. 2014). For example, baits may be consumed by nontarget species, which may potentially have an adverse reaction to the vaccine and may also reduce the availability of baits for the target species (Delahay et al. 2003; Cross et al. 2007). Identifying potential nontarget bait uptake is therefore important when developing a delivery system for oral vaccination (Campbell et al. 2006; Beltrán-Beck et al. 2012). In the case of an oral BCG vaccine for badgers, consumption by cattle would be particularly problematic as this could sensitize individuals to the tuberculin skin test used to detect bTB in cattle, potentially resulting in healthy cattle being diagnosed as having bTB (Buddle et al. 2005).

In badgers, an oral vaccine is most likely to be deployed at the sett (Delahay et al. 2003; Chambers et al. 2014), which is the shared burrow system occupied by a badger social group. Although bait consumption by nontargets was not observed during a small-scale study at two badger setts in Gloucestershire, UK (Cagnacci and Massei 2008), nontargets were suggested as a possible reason for low uptake by badgers in another field trial (Southey et al. 2001).

We used data collected from badger setts which were part of a wider program of work to develop an oral TB vaccine, to investigate nontarget interference of candidate vaccine baits deployed for badgers. The primary aim of the wider bait deployment study was to determine levels of bait uptake by badgers (reported separately) for two differing candidate baits (lipid bait and paste bait), distributed in two different ways (down sett entrances and on the surface), across three areas in southwest England. We used data from a subset of 16 setts where surveillance video cameras had been installed to investigate two simple, but fundamental questions: (1) which nontarget species are likely to be present in close proximity to badger setts across a range of habitats?; (2) if present, which species are likely to consume or otherwise interfere with vaccine baits deployed for badgers. The small number of setts monitored combined with the diversity of local habitat differences within study areas and limited direct evidence of nontargets eating baits prevented an investigation of nontarget interference in relation to study area, bait type, or deployment method.

Methods

Bait deployment

The data collected in the current study derive from an investigation of bait uptake among 48 social groups of wild badgers located within three areas in the UK (Tiverton in Devon, and Cheltenham and Tetbury in Gloucestershire). No baits in this study contained vaccine as the purpose was to assess uptake by badgers (reported separately) and nontarget species of two candidate baits for BCG delivery. The chosen study areas were typical of the lowland pastoral landscape which predominates across those parts of the UK where vaccination of badgers would be most likely to occur. Badger group territories typically contain a main breeding sett which is occupied most of the time, as well as smaller outlying setts which are typically used less often (Roper 2010). In this study, baits were only deployed at main setts, where the majority of oral vaccine baits would most likely be deployed. At each badger sett, one of two bait types was deployed: a peanut-based paste bait (Connovation Ltd. and Pest Tech (PT) Ltd. NZ) deployed at 36 setts and a lipid bait (Immune Solutions Ltd. (ISL), NZ) deployed at 12 setts, both of which were contained within a sealed plastic-lined paper packet (packet dimensions; 100×160-mm PT baits and 76×76-mm ISL baits). A limited number of lipid baits were available; hence, they were only deployed at 12 of the 48 social groups. Baits were either placed down sett entrance holes (“down holes” at 24 setts) or individually in a shallow depression in the ground beneath a 20×20-cm (~2.5 kg) floor tile that could easily be moved by badgers but not by the majority of nontargets (“under tiles” at 24 setts). Fifteen portions of each bait type were deployed daily for 12 consecutive nights at the main sett of each social group

(180 baits per sett). A total of 8640 baits were deployed across the study, 2160 lipid baits and 6480 paste baits. Where baits were deployed under tiles, the number presumed to be taken by badgers (tile moved and bait taken) and nontargets such as rodents (tile not moved but bait taken) were recorded daily, and any uneaten baits were removed. The study was carried out between16th May and 29th July 2011, covering the period when cubs would have recently emerged from setts and when natural food availability is likely to be relatively low (Roper 2010). For logistical reasons, the timing of bait feeding was slightly staggered between the three areas, with baits deployed for a 12-day period at each sett.

Identification of nontarget species

A total of 16 setts were selected from two areas (eight from Cheltenham and eight from Tetbury, Table 1), which were 27 miles apart. Both areas are composed of a highly heterogeneous matrix of farmland (arable and pasture), with fragments of woodland and small urban areas. This is similar to much of southwest England where bTB is problematic and where badger abundance is high. Badger setts were located in a variety of habitat types/locations with the majority located in woodland patches, or in hedgerows and overgrown banks adjacent to farmland. Baits were deployed down holes at half of the selected setts (8) and on the surface under tiles at the remainder (8). A single surveillance camera (assembled by cctvaccess.com, Gloucestershire, UK, resolution=704×576 or higher) with infrared light arrays was placed at each selected sett in a suitable location depending on the treatment. At setts where bait was deployed under tiles, cameras were positioned to monitor between one and four tiles. Cameras at the setts where bait was deployed down entrance holes were positioned to monitor activity in and around the hole with the most evidence of badger activity. While it was not possible to monitor the fate of all baits deployed down holes, some baits at most of the setts could be monitored and cameras were positioned to record entry and/or exit from holes by nontarget species and the presence of species in the immediate vicinity of the sett. Surveillance took place for the duration of bait feeding with cameras being activated in the afternoon immediately after bait had been deployed. Cameras were set to record continuously with equipment checked and batteries replaced daily (between daily bait checks), although this varied slightly.

Table 1 Numbers of badger social groups where cctv surveilance was carried out, labeled by location, bait type, and bait placement method

	Cheltenham		Tetbury		Total
	Under tiles	Down holes	Under tiles	Down holes	
PT Paste	4	3	2	3	12
ISL Lipid		1	2	1	4
Total	4	4	4	4	

An attempt was made to identify all nontarget species observed on camera, but mice, voles, and rats were grouped together as “small rodents.” Because it was not possible to identify individuals, each observation was recorded separately; therefore, multiple observations of the same individual are likely to have been recorded. An “observation” represented an instance where an individual animal was recorded entering and then leaving the field of view of the camera. Individuals were recorded as “interacting with bait” if they were observed sniffing and/or pawing at either the baits or tiles, and as “eating baits” if they were observed consuming or carrying away bait.

Results

Video footage

We collected 3678 h of video footage over 175 nights of surveillance. Cameras recorded between 12 and 24 h of footage per day (mean=21 h). Nontarget species were observed in the vicinity of all 16 badger setts where cameras were deployed, resulting in 2083 separate observations. On average, nontarget observations constituted 65 % of all observations at each sett, although this varied substantially among badger setts (sd=31 %, min=7 %, max=100 %, Table 2).

Across all setts, small rodents were the most commonly observed group of nontargets, with nearly twice as many observations than of badgers (Table 2). While it was not generally possible to identify small rodents to species level with a high degree of certainty, based on their general appearance and local abundance, they most likely included brown rats *Rattus norvegicus*, wood and/or yellow-necked mice *Apodemus* sp., and bank voles *Myodes glareolus*. A wide variety of other species were recorded less frequently, including roe deer *Capreolus capreolus*, muntjac *Muntiacus reevesi*, red fox *Vulpes vulpes*, European rabbit *Oryctolagus cuniculus*, gray squirrel *Sciurus carolinensis*, American mink *Neovison vison*, European brown hare *Lepus europeaus*, ring-necked pheasant *Phasianus colchicus*, domestic dog *Canis familiaris*, and domestic cat *Felis catus* (Table 2). Although these species made up a small proportion of the total sightings, there was wide variation among setts such that they were locally common in some instances (Table 2). Two of the 16 setts were potentially accessible to cattle or other livestock during the study period (baits were placed down holes at both setts); however, these species were not observed in the vicinity of the sett.

Where baits were placed down holes, the only nontarget species observed interacting with them were small rodents and

Table 2 Sightings (% of total and total number of cases) of all species (including badgers) recorded at badger setts where bait was placed either down holes or under tiles

	Bait down holes		Bait under tiles		Total sightings		Variation across setts			
Species	%	n	%	n	%	n	mean %	min %	max %	% setts present
Small rodent	65.1	1061	46.9	671	56.6	1732	51.0	1.79	91.4	100
Badger	26.8	437	37.8	541	32.0	978	34.7	0	93.3	93.8
Rabbit	6.1	99	10.4	149	8.1	248	8.6	0	37.6	56.3
Deer	0.7	12	2	29	1.3	41	2.3	0	8.6	68.8
Squirrel	0.5	8	1.5	21	0.9	29	0.9	0	7.5	43.8
Fox	0.6	9	0.3	4	0.4	13	0.5	0	3.6	37.5
Dog	0.0	0	0.8	12	0.4	12	0.8	0	11.4	18.8
Cat	0.0	0	0.2	3	0.1	3	0.7	0	10.7	6.3
Pheasant	0.1	2	0.1	1	0.1	3	0.4	0	5.7	12.5
Hare	0.1	1	0	0	0	1	0.01	0	0.2	6.3
Mink	0.1	1	0	0	0	1	0.04	0	0.7	6.3
Total sightings		1630		1431		3061				

Also shown are the mean, min, and max percentage of observations where species were recorded across the 16 setts observed, and the percentage of setts where each species was recorded

rabbits (Table 3), and small rodents were the only nontargets observed eating or carrying away baits. Where baits were placed under tiles, small rodents, rabbits, gray squirrels, foxes, domestic cats, and dogs were observed interacting with them or the tiles covering them (Table 3). However, small rodents and gray squirrels were the only nontarget species observed eating or carrying away baits placed under tiles (Table 3). The ISL lipid bait was eaten by rodents on 11 occasions, while the Pest-Tech paste bait was eaten on 49 occasions by small rodents and squirrels. However, the number of setts with camera equipment differed between these two bait types (ISL lipid=4, Pest-Tech paste=12), as did the number of setts where nontargets were observed eating baits (ISL lipid=1, Pest-Tech paste =5); so, it was not possible to conduct a formal comparison.

Table 3 Observations of nontarget species interacting with bait/tiles or eating bait at badger setts where bait was placed down holes or under tiles

	Bait down holes				Bait under tiles			
	Interacting with bait		Eating bait		Interacting with bait		Eating bait	
Species	%	n	%	n	%	n	%	n
Rodent	38.3	406	3.6	38	35.5	238	2.8	19
Rabbit	5.1	5	0	0	26.2	39	0.0	0
Deer	0	0	0	0	0.0	0	0.0	0
Squirrel	0	0	0	0	33.3	7	14.3	3
Fox	0	0	0	0	25.0	1	0	0
Dog	0	0	0	0	8.3	1	0	0
Cat	0	0	0	0	33.3	1	0	0
Pheasant	0	0	0	0	0	0	0	0
Hare	0	0	0	0	0	0	0	0
Mink	0	0	0	0	0	0	0	0
Total		411		38		287		22

Percentages are of observations of each species (Table 1), where each behavior was observed

Bait disappearance from under tiles

Nontargets, such as small rodents and squirrels, took baits at six of the 24 setts where they were placed under tiles, accounting for an estimated 131 out of a total of 4320 deployed baits (3 %). It was not possible to determine whether nontargets may have interfered with baits from under tiles that had been moved by badgers, or what percentage of tiles may have been moved by larger nontargets such as foxes, but there was no evidence of either from the 3678 h of video footage collected. It was not possible to use field signs to identify the species responsible for bait removal from beneath tiles with any degree of certainty, but in the majority of cases, they are likely to have been taken by small rodents, as few other species would have been able to take the baits without first moving the floor tile. At the six setts where baits were taken by nontargets, the number taken varied widely, but constituted a significant proportion of the total number of baits deployed in some cases (mean=11 %, sd=12.4, min=2 %, max=35 %).

Discussion

A vaccine bait would ideally be target species specific, as uptake by nontargets may reduce vaccine coverage in the target population, may have adverse welfare impacts on nontarget species (Cross et al. 2007), and would impact on the costs of vaccine deployment. Unfortunately, creating a species-specific bait is very difficult as many target and nontarget species have overlapping diets. In the case of BCG vaccine, a particular cause for concern would be if cattle consumed baits as they may be sensitized, potentially compromising the tuberculin tests used to detect bTB in cattle (Buddle et al. 2005). In the present study, we found that a significant proportion of wildlife activity recorded close to badger setts was attributable to nontarget species. No cattle were recorded in the proximity of baits deployed for badgers, although cattle only had direct access to two of the setts; potential exposure of baits to cattle is part of ongoing research. The most commonly observed wildlife species were small rodents, which were observed at 100 % of setts and, in some cases, accounted for >90 % of observations at the sett (Table 2). In addition, a total of 11 other nontarget species were observed at badger setts (Table 2), indicating that a broad range of species may potentially come into contact with vaccine baits. Small rodents and rabbits were observed directly interacting with baits deployed down holes, while both these species along with squirrels, foxes, domestic dogs, and cats were observed interacting with baits placed under tiles in the vicinity of the sett. The greater diversity of species interacting with baits under tiles may reflect greater attraction to nontargets for baits deployed in this way. Alternatively, this difference may simply be because species interacting with baits under tiles were more visible compared to those interacting with baits down holes where the majority of baits were not in view of the camera, or there may have been fewer species present at setts where baits were deployed down holes (Table 2). It is, therefore, not possible to determine which method of bait deployment would result in the lowest level of nontarget interaction. Placing cameras closer to sett entrances may provide further data on nontarget interactions inside sett entrances; however, this may also act to deter the target species (badgers), which would be undesirable.

Badger setts occur in a wide variety of locations and habitats (Roper 2010), with setts in the current study situated within hedgerows, fields, and patches of woodland across a mixed and highly variable farmland/woodland landscape. It is, therefore, not surprising that the presence and abundance of nontarget species varied so markedly among the monitored setts (Table 2). Variation among setts in nontarget activity may have been partially influenced by bait type/deployment method and/or location, although the limited sample size means that it was not possible to investigate these factors. The two study areas in the current study (Cheltenham and Tetbury) have similar habitats, which are characteristic of the wider pastoral landscape in south-west England, where badger abundance is high and bovine TB is endemic. The diversity of nontarget species observed in the current study is likely to be similar to the composition of species found across the wider landscape, as all common mammal species/groups were detected on camera (deer, small rodents, foxes, squirrels, rabbits/hares). However, it is possible that in certain localized areas, fine scale environmental factors may result in different levels of nontarget activity and bait interference from that observed in this study. Other than mink, no other small mustelids (e.g., Stoat *Mustela ermine* and Weasel *Mustela nivalis*) were observed, although these species occur at low densities and are obligate carnivores, so are unlikely to consume significant numbers (if any) of the bait types investigated. Similarly, feral wild boar *Sus scrofa* now occur in small naturalized populations in the UK. Although boar do not occur within the current study area, it is possible that in localized areas, they may consume baits deployed for badgers.

Of the six nontarget species observed interacting with baits, only small rodents and squirrels were observed eating baits, being responsible for the consumption of 35 % of bait taken from under tiles at one sett. This indicates the potential for a significant number of baits to be taken by nontargets. Although foxes and dogs were not observed eating baits, uptake by these species seems likely where present, given their omnivorous and opportunistic foraging habits (Harris and Yalden 2008). How nontarget bait consumption would impact on uptake by badgers is unclear, but given that at several setts, small mammals removed >10 % of baits from under tiles, it seems plausible that bait uptake by badgers could be negatively affected in some cases.

Although badgers are the focus of bTB management in the UK, low levels of disease prevalence (typically <5 %) have also been recorded in a broad range of other mammal species, including small rodents, foxes, and deer (Delahay et al. 2007). Consumption of vaccine baits by nontarget species could therefore, in some cases, be considered beneficial, given that BCG has been shown to have a protective effect in mice, deer, and other species (Murphy et al. 2008; Nol et al. 2008), although the level of coverage achieved is likely to be low. While adverse reactions to BCG have been recorded (e.g., cervical lymphadenitis) in mice receiving orally administered BCG (Murphy et al. 2008), such reactions are rare, and BCG has a good safety record across a wide range of species (Murphy et al. 2008). Consequently, the consumption of vaccine baits by nontarget species is unlikely to be of significant welfare or conservation concern.

Orally vaccinated badgers and possums may shed BCG bacilli in their feces for up to 17 days after vaccination (Wedlock et al. 2005; Corner et al. 2010) and so the potential exists for nontarget species to do likewise. The main nontargets observed taking baits in the present study were small mammals, which typically have small home ranges (Attuquayefio et al. 1986) and deposit relatively small amounts of fecal material. It therefore seems unlikely that BCG would be excreted by nontarget wildlife over a large enough area and in sufficient amounts to pose a risk to cattle, which would need to consume high doses (10^8 colony forming units) of BCG to be sensitized (Buddle et al. 2005). Potential excretion of BCG by badgers is being investigated as part of the research and development of an oral TB vaccine for badgers (Chambers et al. 2014).

Bovine TB in cattle is a major problem in parts of the UK and the RoI, and there is intense debate over how best to manage transmission risks from badgers. The English and Welsh Governments, along with the Irish government, have committed to investigate a range of approaches including the development of an oral vaccine for badgers (http://www.defra.gov.uk/ahvla-en/science/bovine-tb/), which will most likely be deployed at badger setts (Delahay et al. 2003; Robinson et al. 2012; Chambers et al. 2014). The present study highlights the potential for a range of nontarget species to come into contact with an oral vaccine deployed at badger setts, and while most nontargets are unlikely to interfere with baits, in some cases, small rodents may consume a considerable number. This could potentially negatively impact on the delivery of a vaccine to a sufficiently high proportion of the badger population. However, current research with candidate vaccine baits suggests that uptake by nontargets will not detrimentally affect the uptake of vaccine baits by badgers (Chambers et al. 2014), and this is the subject of on-going work.

An oral vaccine for badgers is currently under development, alongside potential deployment options. Research to date indicates that an appropriate approach would be to deploy vaccine baits directly down badger setts, which would reduce the likelihood of exposure to cattle and other livestock, and to some other nontarget species. Future oral vaccine development work should continue to assess, and attempt to reduce, the risk of vaccine consumption by nontargets including cattle.

Acknowledgments We thank the National Wildlife Management Centre's Woodchester Park field team for carrying out bait deployment work. We also thank Connovation Ltd., Pest Tech Ltd., Immune Solutions Ltd. and the Department of Bacteriology, APHA, for bait development and production. This study was funded by the UK Department for Environment, Food and Rural Affairs.

References

Attuquayefio D, Gorman M, Wolton R (1986) Home range sizes in the wood mouse Apodemus sylvaticus: habitat, sex and seasonal differences. J Zool 210:45–53

Beltrán-Beck B, Ballesteros C, Vicente J, de la Fuente J, Gortázar C (2012) Progress in oral vaccination against tuberculosis in its main wildlife reservoir in Iberia, the Eurasian wild boar. Vet Med Int 2012:978501

Brown E, Cooney R, Rogers F (2013) Veterinary guidance on the practical use of the Badger BCG tubercolosis vaccine. In Pract 35:143–146

Buddle BM, Aldwell FE, Skinner MA, Lisle GWD, Denis M, Vordermeier HM, Hewinson RG, Wedlock DN (2005) Effect of oral vaccination of cattle with lipid-formulated BCG on immune responses and protection against bovine tuberculosis. Vaccine 23: 3581–3589

Buddle BM, Wedlock DN, Denis M, Vordermeier HM, Hewinson RG (2011) Update on vaccination of cattle and wildlife populations against tuberculosis. Vet Microbiol 151:14–22

Cagnacci F, Massei G (2008) Monitoring bait uptake in badgers: a pilot study using PIT-tag system and time-lapse video surveillance. Ethol Ecol Evol 20:165–171

Campbell T, Lapidge S, Long D (2006) Using baits to deliver pharmaceuticals to feral swine in southern Texas. Wildl Soc Bull 34:1184–1189

Carter SP, Chambers MA, Rushton SP, Shirley MDF, Schuchert P, Pietravalle S, Murray A, Rogers F, Gettinby G, Smith GC, Delahay RJ, Hewinson RG, McDonald RA (2012) BCG vaccination reduces risk of tuberculosis infection in vaccinated badgers and unvaccinated badger cubs. PLoS One 7:49833

Chambers MA, Rogers F, Delahay RJ, Lesellier S, Ashford R, Dalley D, Gowtage S, Davé D, Palmer S, Brewer J (2011) Bacillus Calmette-Guérin vaccination reduces the severity and progression of tuberculosis in badgers. Proc R Soc B Biol Sci 278:1913–1920

Chambers MA, Carter SP, Wilson GJ, Jones G, Brown E, Hewinson RG, 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

Clifton-Hadley R, Wilesmith J, Richards M, Upton P, Johnston S (1995) The occurrence of Mycobacterium bovis infection in cattle in and around an area subject to extensive badger (Meles meles) control. Epidemiol Infect 114:179–194

Corner LL, Costello E, O'Meara D, Lesellier S, Aldwell FE, Singh M, Hewinson RG, 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

Cross ML, Buddle BM, Aldwell FE (2007) The potential of oral vaccines for disease control in wildlife species. Vet J 174:472–480

Delahay RJ, Wilson GJ, Smith GC, Cheeseman CL (2003) Vaccinating badgers (Meles meles) against Mycobacterium bovis: the ecological considerations. Vet J 166:43–51

Delahay R, Smith G, Barlow A, Walker N, Harris A, Clifton-Hadley R, 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

Donnelly CA, Woodroffe R, Cox DR, Bourne FJ, Cheeseman CL, Clifton-hadley RS, Wei G, Gettinby G, Gilks P, Jenkins H, Johnston WT, Fevre AML, Mcinerney JP, Morrison WI (2006) Positive and negative effects of widespread badger culling on tuberculosis in cattle. Nature 439:843–846

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

Harris S, Yalden DW (2008) Mammals of the British Isles: handbook, 4th edn. Mammal Society, Southampton

Krebs J (1997) Bovine tuberculosis in cattle and badgers. In: Ministry of Agriculture, Fisheries and Food, London

Lesellier S, Palmer S, Gowtage-Sequiera S, Ashford R, Dalley D, Davé D, Weyer U, Salguero FJ, Nunez A, Crawshaw T, Corner LL, Hewinson RG, Chambers MA (2011) Protection of Eurasian badgers (Meles meles) from tuberculosis after intra-muscular vaccination with different doses of BCG. Vaccine 29:3782–3790

Murphy DA, Corner LAL, Gormley E (2008) Adverse reactions to Mycobacterium bovis bacille Calmette – Guerin (BCG) vaccination against tuberculosis in humans, veterinary animals and wildlife species. Tuberculosis 84:344–357

Nol P, Palmer MV, Waters WR, Aldwell FE, Buddle BM, Triantis JM, Linke LM, Phillips GE, Thacker TC, Rhyan JC, Dunbar MR, Salman MD (2008) Efficacy of oral and parenteral routes of Mycobacterium bovis bacille Calmette-Guerin vaccination against experimental bovine tuberculosis in white-tailed deer (Odocoileus virginianus): a feasibility study. J Wild Dis 44:247–259

Palmer MV, Thacker TC, Waters WR, Gortázar C, Corner LaL (2012) Mycobacterium bovis: a model pathogen at the interface of livestock, wildlife, and humans. Vet Med Int 2012:236205

Robinson PA, Corner LAL, Courcier EA, McNair J, Artois M, Menzies FD, Da A (2012) BCG vaccination against tuberculosis in European badgers (Meles meles): a review. Comparative immunology, microbiology and infectious diseases. Comp Immunol Microbiol Infect Dis 35:277–287

Roper T (2010) Badger, vol 114. HarperCollins, UK

Southey A, Sleeman D, Prendergast J, O'Sullivan R, Mulcahy M (2001) Use of biomarkers to assess the feasibility of delivering a vaccine to badgers (Meles meles). J Zool 253:133–139

Tompkins DM, Buddle BM, Whitford J, Cross ML, Yates GF, Lambeth MR, Nugent G (2013) Sustained protection against tuberculosis conferred to a wildlife host by single dose oral vaccination. Vaccine 31:893–899

Wedlock D, Aldwell F, Keen D, Skinner M, Buddle B (2005) Oral vaccination of brushtail possums (Trichosurus vulpecula) with BCG: immune responses, persistence of BCG in lymphoid organs and excretion in faeces. N Z Vet J 53:301–306

White P, Whiting S (2000) Public attitudes towards badger culling to control bovine tuberculosis in cattle. Vet Rec 147:179–184