Bovine TB: a review of badger-to-cattle transmission

Adrian R. Allen
Robin A. Skuce
Stanley W. J. McDowell

Bacteriology Branch
Veterinary Sciences Division
Agri-food and Biosciences Institute

31 March 2011

Please cite as: Allen AR, Skuce RA, McDowell SWJ (2011). Bovine TB (TB): a review of badger-to-cattle transmission.
http://www.dardni.gov.uk

1 Executive summary:

1.1 Badger-cattle transmission – the evidence.

A. Eurasian badgers (*Meles meles*) have been implicated as a potential source of *Mycobacterium bovis* for cattle since an infected badger was identified in GB in 1971. The evidence base which supports a role for infectious badgers in bovine tuberculosis (TB) epidemiology includes the following observations:

1. Badgers in the wild are susceptible to *M. bovis* infection and can develop TB disease pathology sufficient to support the natural history of *M. bovis* although, importantly, it is not clear whether TB is self-sustaining in the badger population. Captive wild badgers can also be experimentally-infected by several routes.
2. The routes of transmission proposed between badgers and cattle (predominantly direct aerosol infection) are plausible given the current understanding of the badger-cattle interface.
3. Epidemiological studies have indicated an association between TB in badgers and TB in cattle.
4. Molecular typing data supports a local epidemiological association between *M. bovis* in cattle and badgers. Badgers and cattle tend to share the same *M. bovis* genotype in the same area. This was evident in NI data (Road Traffic Accident badger study), GB data (Randomised Badger Culling Trial) and ROI data (Four Areas Trial).
5. Experimental infection studies in the early 1970s demonstrated badger-cattle transmission, although inefficient and in a relatively unnatural setting.
6. Badger culling trials conducted in GB and the ROI demonstrated indirectly that badgers contribute to the occurrence of TB in cattle. However, even with these large scale, expensive trials it has not been possible, and it may not be possible, to accurately quantify the extent of transmission between badgers and cattle, or indeed *vice versa*.

B. The maintenance and spread of *M. bovis* infection, within and between populations of cattle and wildlife, is relatively poorly understood. Recent evidence suggests that inter- and intra-regional differences in badger density and/or ecology can affect the mobility of individual badgers and the social structure of groups. This could affect the interaction between cattle and badgers and thereby modulate contact and transmission between the species. To date, no definitive study demonstrating how such variation affects the incidence of TB in cattle has been reported. Hence, it is plausible that the risk of badger-cattle transmission is likely to vary across different geographical regions and over time due to multiple, as yet ill-defined, variables.

1.2 How does it happen?

C. Much of the current understanding of the routes of *M. bovis* transmission between badgers and cattle derives from **pathological** and **ecological** studies. Two potential routes of transmission are identified: (a) **direct** aerosol / respiratory transmission, which may occur when there is close (2-3m) contact and (b) **indirect** transmission through cattle contact with potentially infectious badger excreta such as sputum, pus, faeces or urine. Both direct and indirect transmission routes may potentially occur at pasture and/or in farm buildings.

D. While potential routes of infection have been identified, studies to date have been unable to quantify their relative importance. Previously, direct (or close) contact between the two species was considered to be rare. Therefore, indirect transmission was perceived to pose the greater risk. However, TB is primarily a respiratory infection spread by the aerosolisation and inhalation of bacilli from infectious cases. Recent ecological studies in GB, involving CCTV and proximity logging transponders, revealed that direct badger-cattle contact occurred more frequently than was previously suspected. Whilst there is no firm field evidence, the combination of knowledge of TB pathology in the two species and ecological studies in relation to badger-cattle contacts suggest that direct respiratory transmission is likely to be main route of infection.

1.3 How could badger-cattle transmission be minimised?

Based on the potential transmission routes, a range of interventions have been proposed, including:

1. Preventing direct and indirect transmission in farm buildings through measures to stop badgers gaining access to cattle houses, feed and forage stores (see section 4.2).
2. Much of the advice in relation to intervention at pasture is aimed primarily at preventing indirect contact between badgers and cattle (see section 4.1). Preventing direct contact at pasture is accepted as being particularly difficult.

Several studies have identified, summarised and reviewed potential risk factors for transmission at the badger-cattle interface. However, it is notable that none have been able to provide a risk ranking. If perceived differences in badger ecology by region translate into differences in badger-cattle contact, it is conceivable that bovine TB transmission routes and settings may also vary in space and time. Overall it is suggested, in GB at least, that the physical exclusion of badgers from farm buildings is likely to be the simplest and most practical means to implement (Ward et al, 2010). However, there is a lack of equivalent ecological studies to examine local badger-cattle contacts.

1.4 Factors likely to commend further beneficial study

More generally, the following factors are likely to commend further beneficial study:

1. Given the different climate of Ireland, the different badger diet and the proposed effect that reduced badger density has on increasing ranging, it is conceivable that badger visitation to farmyards in Ireland may be somewhat different to that experienced in GB. We recommend that active surveillance (data-loggers, proximity meters, CCTV etc) and quantification of badger incursions to farms should be undertaken in NI to provide evidence of the risk locally.
2. Furthermore, efforts to gain a greater understanding of the ecology, population and social structure of badgers across Northern Ireland would be beneficial alongside epidemiological analysis to determine how variation in such parameters could affect cattle-badger interactions and inter-species disease transmission.
3. Research should be undertaken in relation to the optimum methods by which biosecurity advice to farmers could be delivered and the parameters that influence farmer uptake of bio-security and husbandry advice. Irrespective of whether or not badger intervention occurs in NI, bio-security steps to minimise contact and transmission at the badger-cattle interface have an important role to play. We therefore recommend that the bio-security advice provided to farmers is reviewed to ensure that it reflects best practice. As part of that, we feel it is important that expectations are managed effectively and that the complexities of the epidemiology of bovine TB are communicated.
4. In light of recent GB and ROI data on TB pathology in culled badgers (which indicates a predominantly respiratory route of

transmission), we recommend that the methods used for the current RTA study are reviewed.

5. Depending on the results of 1-3 above, and the current TB Bio-security Study, further field trials of practical husbandry-based measures may be warranted. Considering the scale that may be required, it is likely that such studies would focus on the practicality of measures and indirect outcomes such as badger-cattle contacts rather than directly assessing effect on bovine TB occurrence.
6. Much of the work on badger-cattle interfaces has been conducted in GB. At a fundamental level, the rational application of mathematical modelling, using NI-specific parameters, where possible, may help to formulate region-specific intervention studies and advice.
7. Molecular typing has shown the striking geographical clustering and epidemiological association in *M. bovis* genotypes in both cattle and badgers. This suggests that transmission between badgers and cattle occurs, but cannot determine the direction of such transmission, nor the extent of the badger or cattle component in generating the association at any scale. However, current molecular typing approaches can accurately identify epidemiologically-linked cases involving cattle and badgers in a given area. New modelling approaches, which integrate epidemiological (test and movement) and pathogen genotype (genome sequence and family tree) data have the potential to inform on the most plausible sequence of transmission events within an outbreak. We recommend evaluation of these new 'phylo-dynamics' approaches to investigate transmission at the badger-cattle and cattle-cattle interfaces in selected outbreaks.

8. It would be beneficial to undertake a province-wide survey in which badger populations, ecology and behaviour and their effects on badger–cattle contact at pasture or in animal housing could be assessed. Making use of telemetry and/or data logging cattle and badger collars could determine primary badger – cattle interfaces and their variation.

2 Review title and terms of reference

A review of transmission of bovine TB with particular reference to badger-to-cattle spread (a) in cattle housing, and (b) at pasture. This review should also seek from published work or work nearing completion to identify, summarise and rank those badger-cattle interfaces most likely to lead to bovine TB transmission. The review should similarly seek to identify, summarise and rank those practical management actions that could best mitigate the risk of transmission in housing and at pasture and identify any other factors likely to commend further beneficial study.
[DARD Animal Health and Welfare Branch 2010]

2.1 Methods

This review was written after an extensive review of the available scientific literature. On-line resources (PubMed and Web of Science), were used to find appropriate peer-reviewed literature.

PubMed (http://www.ncbi.nlm.nih.gov/pubmed) comprises more than 20 million citations for biomedical literature from MEDLINE, life science journals, and online books.

The DEFRA web-pages on bovine TB and the Final Report of the Independent Scientific Group (ISG, 2007), '*Bovine TB: the Scientific Evidence*' were referenced throughout.

Search terms used included – TB, badgers, badger ecology, pasture, animal housing.

The following relevant areas have been discussed:

- The badger as a maintenance or spill-over host for TB.
- Badger ecology and behaviour – towards a greater appreciation of the role of the badger in transmission of TB to cattle and evidence for cattle-to-badger transmission.
- TB (*M. bovis*) in badgers - effects on ecology and behaviour - and how disease in the wildlife population may affect interactions with livestock.
- What does the pathology of TB in badgers indicate about the most likely transmission routes from wildlife to cattle?
- What interventions would likely reduce the probability of transmission?

- Direct and indirect contact between badgers and cattle at pasture.
- Direct and indirect contact between badgers and cattle in farm animal housing.
- Mitigation strategies which might be taken to limit direct or indirect exposure of cattle to infectious wildlife or their excreta in order to reduce or prevent transmission.

3 Background: Evidence for badger-to-cattle transmission of TB.

Badger-cattle transmission of *Mycobacterium bovis* is invoked as a primary reason for the failure of cattle TB eradication schemes across the UK and Ireland. Uncertainty remains on the exact contribution this route of infection makes to the overall incidence of the disease in cattle (see later). The evidence base which supports a role for infectious badgers in bovine TB epidemiology derives from a combination of sources and includes the following observations:

1. Badgers are susceptible to *M. bovis* infection experimentally and in the wild and can develop TB disease pathology sufficient to support the natural history of *M. bovis*.
2. The routes of transmission proposed between badgers and cattle (predominantly direct aerosol infection) are plausible.
3. Epidemiological studies have indicated an association between TB in badgers and TB in cattle.
4. Molecular typing data supports a local epidemiological association between *M. bovis* in cattle and badgers. Badgers and cattle tend to share the same genotype of *M. bovis* in the same area. This was evident in NI data, GB data and ROI data.
5. Experimental infection studies in the early 1970s demonstrated badger-cattle transmission, although inefficient and in an unnatural setting.
6. Badger culling trials conducted in GB and the ROI demonstrated indirectly that badgers contribute to the occurrence of TB in cattle. However, even with these large scale and expensive trials it has not been possible, and it may not be possible, to accurately quantify the extent of transmission between badgers and cattle, or indeed *vice versa*.

3.1 Early indications of a maintenance host in wildlife

The UK national bovine TB eradication policy, involving diagnostic testing and slaughter of infected cattle, began in 1950, and was initially highly successful (Krebs 1997) in reducing the annual number and incidence of test reactor cattle from nearly 15,000 in 1961 to 569 in 1982 (based on Smith *et al.*, 2006). The annual herd-level incidence was <0.5% and animal-level prevalence was 0.06% at its lowest. However, infection persisted in southwest Britain, leading to speculation that maybe another host was maintaining infection in those areas.

Mycobacterium bovis infection in badgers was first observed in Switzerland in 1957 (Bouvier *et al.,* 1957). Subsequently, in GB in 1971, infected badgers were discovered on farmland in Gloucestershire which had experienced persistent cattle breakdowns (Muirhead *et al.,* 1974). With time, more infected badgers were discovered across many counties in southwest GB (MAFF Reports 1976, 1977, 1979 and 1981, Gallagher and Clifton-Hadley, 2000), the ROI (Noonan *et al.,* 1975) and NI (DANI Report 1978).

These findings, from diverse locations across the British Isles, indicated that badgers were susceptible to TB (*M. bovis*) and potentially constituted a wildlife reservoir which might transmit *M. bovis* infection to cattle (Little *et al.,* 1982). Crucially, it is not known whether TB is self-sustaining in badgers (SGM, 2008). The only evidence, which is anecdotal due to small sample sizes, is the detection of TB in RTA badgers outside RBCT areas (SGM, 2008). Modelling suggests that TB could persist in badger social groups comprising at least six adults and juveniles (White and Harris 1995). Persistence of TB in badgers in Woodchester Park is insufficient evidence since the area probably still has infectious cattle sources. The SGM concluded that if TB was indeed self-sustaining in badgers, cattle-based control measures alone would not eliminate the disease in either species (SGM 2009). We propose that it may be that the ability of badgers to sustain infection in their own populations is variable across different geographical areas as a function of the differing population densities that can occur, as discussed previously. If this was the case, and in some sub-populations badgers did not sustain infection on their own, this could lead to recommending different regional control strategies.

In NI, two studies, one a case control questionnaire, the other a field study have associated sett presence and badger activity with increased TB incidence in cattle (Denny and Wilesmith, 1999; Menzies *et al.,* 2011). The former authors attribute 40% of cattle TB cases in NI to badger activity. These studies, whilst informative, demonstrate only association, not causation, and may be subject to the reporting bias of farmers who have experienced herd TB breakdowns being more likely to report badger activity (Menzies *et al.,* 2011).

3.2 *M. bovis* strain sub-typing.

Pathogen (*M. bovis*) genetic variation, arising naturally by mutation, can be used to differentiate isolates. Two types of strain typing are commonly used for *M. bovis* – spoligotyping (Durr et al., 2000) and variable number of tandem repeat (VNTR) genotyping (Skuce *et al.,* 2005).

When these genotyping techniques are applied to field data from Northern Ireland, a striking geographical clustering of isolates with the same genotypes is observed (Skuce *et al.,* 2010). Similar geographical clustering of *M. bovis* genotypes is also observed in GB (Smith *et al.,* 2006) and also in human cases of TB (*M. tuberculosis*) (Gagneux and Small, 2007). These findings indicate that the bovine TB epidemic (in GB and NI at least) can be viewed as a series of mini-epidemics (Smith *et al.,* 2003) largely maintained by local sources of infection (Skuce *et al.,* 2010) involving either wildlife-cattle and/or cattle-cattle transmission (ISG, 2007).

It has also been observed that the *M. bovis* strain types isolated from cattle and badgers in the same area exhibit a high degree of similarity. The latter has been observed in GB (Woodroffe *et al.,* 2009a) and the ROI (Olea-Popelka *et al.,* 2005) and also in NI (RTA, unpublished). These data indicate that cattle infection and badger infection are epidemiologically-associated and suggest that transmission occurs between them. However, this association does not inform on the direction or routes of transmission (wildlife-cattle versus cattle-cattle).

3.3 Badger culling.

The Krebs report led to the formation of the Independent Scientific Group (ISG), which was tasked with conducting a randomised badger culling trial (RBCT) in England (ISG, 1999) over a five year period in ten separate locations where there was high risk of bovine TB in cattle. At these ten locations, three ‘treatments’ were randomly-assigned to separate land parcels of similar size (~100km^2) – reactive badger culling (culling on accessible land close to a recent herd TB breakdown), proactive culling (culling on accessible land in the defined culling area) and a no culling control area.

The conclusions of the final ISG report (ISG, 2007) indicated that reactive badger culling as conducted, in response to herd breakdowns, actually led to an increase in bovine TB incidence in the geographic area of the cull by 27% (95% CI 2.4% decrease to 65% increase) compared to survey only (no cull) control areas (Donnelly *et al.,* 2003; ISG 2007). Consequently, the reactive culling element was terminated prematurely. The most recent re-analysis of RBCT reactive cull data has demonstrated that the presence of any reactive culling in the previous year within one kilometre of a herd more than doubled the local risk of bovine TB, even after adjusting for the number of confirmed outbreaks nearby. The number of badgers culled in the vicinity of the herd was also associated with increased bovine TB risk (Vial and Donnelly 2011).

Proactive culling, as undertaken by the ISG, recorded a 23% decrease (95% CI 12.4-32.7%) in cattle breakdowns within the culling area when compared to survey only control areas (ISG 2007; Donnelly *et al.,* 2007) over the five year culling period. However, on land up to 2km outside of the proactive cull areas, TB incidence in cattle was increased by 24.5% (95% CI 0.6% lower to 56.0% higher) in comparison to land outside of survey only areas (ISG, 2007; Donnelly *et al.,* 2007) thereby negating any beneficial effect within the culling area. It was proposed that this negative effect was caused by cull-induced disruption of the social and spatial organisation of territorial badger populations – the so-called 'perturbation' effect (Donnelly *et al.,* 2003; ISG, 2007). This social perturbation of the badger population was hypothesised to lead to increased contact at outlying areas between infectious wildlife and cattle.

Subsequently, former ISG researchers have continued to monitor the impacts of RBCT treatments beyond the end of proactive culling. They conclude from ongoing surveillance that data are *"...consistent with an ongoing, but diminishing (test for temporal trend p=0.008), benefit of proactive culling continuing through the latest 6-month period analysed (55 to 60 months post-trial). The effects observed outside trial areas remained consistent with no ongoing effects of proactive culling in these areas. The post-trial results must, of course, be considered in the context of the smaller reduction seen inside proactive trial areas and the increased incidence seen outside proactive trial areas in the period from the end of the initial proactive cull until one year after the last proactive cull in each triplet. From the start of the RBCT to 28 August 2011, incidence of confirmed breakdowns in proactive culling areas was 25.7% lower (95% CI: 18.7% to 32.2% lower) than in survey-only areas.*

In areas up to 2km outside the trial area boundary of proactive culling areas, incidence of confirmed breakdowns was 7.6% higher (95% CI: 14.2% lower to 35.1% higher) than in areas up to 2km outside survey-only areas."

Consequently, former ISG members maintain that GB-wide culling would not be cost effective and would be unlikely to contribute effectively to bovine TB control in cattle and that at the local level *"...detailed consideration is needed to determine whether and where proactive badger culling could be an effective part of bTB control in England and Wales*" (Jenkins *et al.,* 2010; Vial *et al.,* 2011).

Much anticipated data from the ROI had already indicated that proactive culling could contribute to a decline in herd breakdowns within the cull area (Kelly *et al.,* 2008). The East Offaly study (Eves, 1999) reported a 26% decrease in cattle TB incidence inside cull areas. Similarly, the Four Areas Trial conducted in areas of Cork, Monaghan, Donegal and Kilkenny (Griffin *et al.,* 2005) reported an average reduction across all four areas of 60.5% over the five year trial. A perturbation effect was not detectable in these ROI studies (Corner et al., 2008).

Regardless of the subsequent debate about perturbation and its effect on cattle breakdowns in areas outside cull zones, these studies indicate that large well-planned and executed proactive badger culls can reduce disease incidence in cattle herds within culling regions, thereby providing indirect evidence that badgers are involved in the transmission of *M. bovis* to cattle. However, the wide confidence intervals observed in all these studies reflect the relatively small study sizes and the operational difficulties of undertaking them and managing the expectations that they will provide complete answers. In order to detect and monitor any effect, and any regional/temporal variation, the scale required is prohibitive in most cases.

Consequently and because the RBCT was focussed in SW England, Woodroffe *et al* (2005) stress that RBCT data should not be used to evaluate a general GB-wide estimation of the importance of badger-to-cattle transmission. Indeed, the Society for General Microbiology (SGM), in their DEFRA-commissioned independent review of bovine TB research (SGM, 2009), concluded that whilst it would be important to determine the relative importance of specific routes of transmission between species, this was not currently possible, except in a very rudimentary way. At a fundamental level, the badger-cattle component of disease transmission may be highly variable, depending on the structure and nature of infectious contacts.

3.4 Experimental Infections.

Experimentally- and naturally-infected badgers can transmit bovine TB to healthy calves with which they were housed. All 8 calves exposed experimentally to diseased badgers (*M. bovis* isolated from faeces) showed signs of exposure/infection (responsiveness to the comparative tuberculin skin test) within ~6 months of continuous exposure (Little *et al.,* 1982). Post-slaughter, the calves exhibited tuberculous lesions in retropharyngeal lymph nodes and bronchi, from which *M. bovis* was isolated (Little *et al.,* 1982). These findings confirmed that badger-to-cattle TB transmission was possible (proposed to be most likely indirect via water and/or hay), although not particularly efficient. We did not find evidence that these initial studies had been repeated in GB or elsewhere.

3.5 Plausibility of a role for badgers in infecting cattle.

See section 3.2.2 for in depth review. Typically, the disease in both cattle and badgers is similar, with most pathology observed in the lungs and associated lymph nodes (Gallagher and Clifton-Hadley 2000). These data confirm the largely respiratory nature of the disease in both animals and suggest that aerosol transmission is a potential major route for inter-species infection.

4 Possible Routes of Transmission from badgers to cattle.

Potential routes of transmission have been investigated indirectly using ecological and behavioural studies of healthy and diseased badgers. Pathological studies in badgers help to inform on the most likely transmission routes. Ecological studies inform on the settings where such transmission might be occurring.

4.1 Badger ecology

The Eurasian badger (*Meles meles*), which shares its preferred habitat with many domesticated, wild and feral animals, is the largest carnivore in the British Isles. It is mainly nocturnal (Mullineaux, 2003) and lives in social groups of typically five animals (range 2-35 in GB, Neal and Cheeseman, 1996). Each social group will generally have one main sett within its territory, with occasional, additional, smaller setts observed (Mullineaux, 2003).

In GB, in the late 1990s the badger population was estimated to be ~300,000 (Wilson *et al.*, 1997, Clarke *et al.*, 1998, cited by Connor *et al.,* 2009) with a mean density of 5.44 setts per km^2 and 3.2 badgers per km^2 in the RBCT areas (ISG, 2007). A province-wide average of 3.29 setts per km^2 (0.56 active badgers setts per km^2) and ~2-4 badgers per km^2 was reported for NI (DARD, 2008). The ROI badger population is at a lower density than in GB. Data from the Four Areas culling trial indicated that pre-cull there was a mean density of 2.5 setts per km^2 and ~2 badgers per km^2 (Griffin *et al.,* 2005; ISG, 2007; Sleeman *et al.,* 2009; O'Connor *et al.,* 2009).

Social groups are typically of mixed sex with all individuals interacting closely. This can lead to intra-group conflict to assert dominance, which may lead to bite wounds (Macdonald *et al.,* 2004). Similarly, animals from different social groups can inflict wounds on each other during territorial disputes (Neal and Cheeseman, 1996). In general, excursions of one social group to the adjoining territory of another group is common (Woodroffe *et al.,* 1993) and appears to be undertaken principally for mating (Carpenter *et al.,* 2005). However, in dense populations like Woodchester Park, the RBCT sites, and others typically seen in south west Britain, badger movement appears to be greatly reduced with evidence for higher levels of territoriality (MacDonald *et al.,* 2006).

Time of emergence from setts and frequency of excursions tend to be dictated by light intensity, weather conditions and food availability (Neal and Cheeseman, 1996). Whilst they do not hibernate, badger activity is greatly reduced between November and February (Mullineaux, 2003). Badgers are generally opportunistic omnivores; they do most of their feeding by nocturnal foraging between sunset and dusk (Mullineaux, 2003). By far the largest and most important component of their diet, at least in southwest GB, is the earthworm (Neal, 1988; Corner *et al.,* 2010) for which they forage. However, being opportunists, their diet differs by territory and season, encompassing insects and invertebrates, small mammals, birds eggs, fruits and seeds and typically whatever is available in their territory (Mullineaux, 2003; Corner *et al.,* 2010).

The preferred badger habitat in GB is well-drained soil close to deciduous and mixed woodland (Clements et al., 1988), bordering large areas of grassland (Wilson *et al.,* 1997), coincidentally the land most favoured in the UK and Ireland for cattle grazing. Wilson *et al* (1997) proposed that historical expansion of good quality pasture for cattle grazing increased the territory available for badgers to forage for earthworms. Well-marked paths between setts, latrines and main feeding areas are clearly visible within social group territory, with latrines, and urine scent marking principally found on territorial boundaries (Neal and Cheeseman, 1996), which coincide with near linear landscape features such as field edges bounded by hedges, fences and walls (Ward *et al.,* 2010).

Potential differences in badger ecology between GB and Ireland have been suggested (Feore, 1994) and may have an impact on the epidemiology of *M. bovis* infection both within badger populations and between badgers and cattle (Olea Popelka *et al.,* 2005). In the ROI, the estimated badger population size is considerably smaller than in GB at ~72,000-95,000 animals (Sleeman *et al.,* 2009). This is approximately half of a previous estimate (Smal 1995). Sleeman *et al* (2009) suggest that this decline may be the result of greater urbanisation and increased car use from 1990s onwards leading to greater badger deaths in road traffic accidents (RTA).

A suggested possible consequence of this reduced badger population and lower density has been increased ranging behaviour in ROI badgers compared to those in densely populated areas of GB (Kelly and More, 2010). In a less densely populated area of GB, North Nibley, this phenomenon has been observed with extra territorial excursions being negatively correlated to higher population density (Tuyttens *et al.,* 2000). DAFF has indicated that badgers can travel up to 15km in declining populations (DAFF, 1996).

Potential differences in ecology between GB and ROI are being investigated in relation to the perceived differences in outcome of culling trials (O'Connor *et al.,* 2009). In NI and ROI badgers have been reported to frequently visit and take over neighbouring main setts (Sleeman, 1992; O'Corry-Crowe *et al.,* 1993; Feore and Montgomery, 1999). Reduced badger numbers may lead to a greater number of unoccupied setts which reduces territoriality and increases ranging (Sleeman *et al.,* 2009). For example, in the ROI 41% of all setts in the Four Areas trial were unoccupied (Sleeman *et al.,* 2009).

Initially in ROI, unlike in GB and NI, no spatial association between infected badgers and cattle with the same *M.* bovis strain was observed (Olea-Popelka *et al.,* 2005) and multiple strains were isolated from some setts, including strains not seen in local cattle. This suggested that badgers from different areas where another strain predominates were moving freely into other areas and bringing infection with them (Olea-Popelka *et al.,* 2005; Costello *et al.,* 2006; Kelly *et al.,* 2010). Olea-Popelka *et al* (2006) consider that this finding may have resulted from pre-trial disturbance and ranging of the existing badger population due to badger removal. Olea-Popelka *et al.* (2005) speculate that even in undisturbed populations, movement in response to low population density may occur (Olea-Popelka *et al.,* 2005). However, a more recent re-analysis of the spatial data from the FAT arrived at a different conclusion. Widespread spatial association was detected between badger and cattle strains in all areas, except Donegal (Kelly *et al.,* 2010).

Badger populations in the UK and ROI are closely associated with good quality pasture. In the ROI badger setts are most commonly found at field boundaries such as hedgerows. In GB the preferred badger habitat is woodland (Sleeman *et al.,* 2009). The diet of badgers in ROI has been reported to differ somewhat from GB, with earthworms not contributing substantially to their diet (Corner *et al.,* 2010). Indeed, whilst still occupying a narrow niche, the diet of ROI badgers appears to be more diverse than in GB and is season-dependent, including a range of larvae, amphibians and insects (Cleary *et al.,* 2009).

In NI, a badger population survey in 2007/2008 reported an average density of 0.56 social groups per km^2 and an estimated total abundance of 7,500 badger social groups. The total number of badgers was estimated at 33,500 with an average number of 4.5 animals per social group (Reid *et al.,* 2008). There was a distinct gradient across NI, with most badgers found in counties Armagh and Down. Due to reduced forestation in NI, badger setts were more likely to occur in shaded hedgerows (Reid *et al.,* 2008) and on or close to good quality pasture land (Menzies *et al.,* 2011). Neither average badger density nor overall population size in NI had changed significantly since last surveyed (Feore, 1994), in contrast to GB where surveys indicated substantial increases in the badger population (Cresswell *et al.,* 1990; Wilson *et al.,* 1997; Macdonald and Newman, 2002).

In general, it seems that there is a continuum of variation in badger ecology which is region-dependent and reflects the density of animals in the landscape (Cresswell and Harris, 1988; Hutchings *et al.,* 2002) and the different prey biomass available in different environments and areas which will dictate their carrying capacity (Kruuk and Parish, 1982). The available data and publications do show that this reduced density has an effect on badger movement and territoriality. Even within large areas of the same landscape, there can be an observable difference in local badger ecology and density. This has been noted in both ROI and GB (Murphy *et al.,* 2011; MacDonald *et al.,* 2006). However, a definitive study which investigates the relationship such increased ranging may have on TB epidemiology in cattle and badgers, does not appear to have been undertaken yet.

This heterogeneity in badger ecology and resulting population densities may well have an effect on the epidemiology of TB infection in badgers and consequently in transmission of TB to cattle. Reduced badger population density could result in lower contacts between infectious animals and hence reduced transmission between badgers and potentially badgers and cattle (Murphy *et al.,* 2011; Sleeman and Mulcahy, 2005). However if reduced population density results in reduced territoriality and wider ranging in the badger population, could this actually increase contacts and transmission? Woodroffe *et al* (2009b) have demonstrated that lower population density in badgers is associated with increased badger TB prevalence in GB.

Perhaps there is a balance between ecological factors and the resulting burden of disease which itself varies in different localities and which may dictate different control schemes for different areas (Kelly *et al.,* 2010). To date it appears that no definitive evidence of the exact relationships between differing badger ecology and TB prevalence have been produced.

4.2 TB in badgers – Pathology and Epidemiology.

4.2.1 Badger TB prevalence.

Prevalence of *M. bovis* infection in badger populations may be sought as base-line data, although it is likely to vary by region and over time and is recognised as being difficult to quantify accurately (SGM, 2008). Standard pathology investigations have limited sensitivity (ISG, 2007) with the result that prevalence is likely to be underestimated. Recent investigations indicate that more detailed *post-mortem* examinations result in the detection of microscopic lesions that would otherwise evade detection by standard procedures (Jenkins *et al.,* 2008b; Cranshaw *et al.,* 2008; Murphy *et al.,* 2010).

Badgers killed in road traffic accidents (RTA) have proven to be a useful source of data in attempting to determine badger TB prevalence at a county-wide scale (ISG, 2007). The ISG reported that standard *post mortem* examination revealed that 15% of GB RTA badgers had TB (ISG, 2007). The ISG cautioned, however, that at a localised level below county size, owing to reduced availability of RTA badgers, this method may not be sufficient for surveillance (ISG, 2007). Similar RTA data collected in NI indicated that ~20% of badgers were infected (Abernethy *et al.,* 2010). In GB, the ISG reported that in proactive cull regions, 16.6% of badgers were tuberculous (ISG, 2007) whilst in reactive cull regions this figure was 14.9% (Woodroffe *et al.,* 2009a).

Similarly, studies in the ROI indicated that, by the standard protocol, culled badger TB prevalence was 12.1% (Murphy *et al.,* 2010) and largely in agreement with RTA figures. More thorough *post mortem* examination of culled badgers led to the detection of an increased number of infected animals. Cranshaw *et al.* (2008) demonstrated that, in GB, proactively culled RBCT badgers had a true prevalence of TB infection of 24.2%. Similarly, in the ROI, more detailed *post-mortem* examination of culled badgers from across the country revealed a prevalence of 36.3% (Murphy *et al.,* 2010).

Using cage trapping, anaesthesia and live sampling of badgers Drewe *et al* (2010) used latent class analysis to estimate the outcome of multiple tests on live badgers (culture, gamma interferon and Stat-Pak ELISA), in the absence of a perfect gold standard diagnosis. Sensitivity of diagnostic testing was estimated at ~93% and badger TB prevalence was estimated subsequently as 20.8% in Woodchester Park, Gloucester (Drewe *et al.,* 2010).

Woodroffe *et al* (2009b) showed, rather counter-intuitively, that *M. bovis* prevalence was actually higher in less dense groups than in higher density groups, with a higher prevalence among recently immigrating animals. Smaller badger populations and increased ranging may lead to increased contacts and disease transmission. Intra-regional, inter-regional and temporal differences in badger TB prevalence are to be expected owing to the potential differences in ecology and population dynamics of both cattle and badgers in different areas as illustrated recently in the ROI (Murphy *et al.,* 2011). Regardless of 'true' prevalence, these studies indicate that a significant component of the badger population across the UK and Republic of Ireland is infected with *M. bovis*.

4.2.2 The pathology of badger TB: Potential routes of transmission.

The gross pathology of TB in badgers exhibits substantial heterogeneity, with most badgers showing little or no obvious signs of disease. The majority of badgers exhibiting pathology had lesions in the respiratory tract (Clifton Hadley *et al.,* 1993; Gallagher and Clifton-Hadley, 2000; Murphy *et al.,* 2010). This observation is significant and suggests that in badgers (as in cattle and humans) 'TB' is primarily a respiratory disease.

Corner *et al* (2007) described an endo-bronchial infection model for badgers. They showed that lesions of TB were observed in all badgers inoculated with high and medium doses and that *M. bovis* was cultured from these infected badgers. They concluded that badgers appeared to control and limit such infection. A subsequent study demonstrated that infection was relatively non-progressive and that dissemination, when it occurred, was limited to the hepatic and mesenteric lymph nodes (Corner *et al.*, 2008). More recently, 215 ROI badgers were examined using an enhanced post-mortem protocol (Murphy *et al.*, 2010). They report that infection prevalence was approximately three-fold higher using this protocol. As in other studies, the thoracic cavity (lungs and pulmonary lymph nodes) was found to be the most common infection site.

The ISG presented a summary of *post-mortem* findings in a sample (N=493) of badgers culled in the RBCT (ISG 2007, table 4.12, p77). Lesions of TB were distributed as follows: head 28%, lung 34%, chest 43%, abdomen 23% and peripheral sites 24% (since lesions may have been detected in more than one compartment, these figures do not sum to 100%). This illustrates the primacy of the head/lung/chest sites in TB pathology in badgers. Commenting on the potential for generalised TB to create the alleged 'super-excretor' badger, they concluded that the number of such badgers was very low in the RBCT data (199 of 9,919= 1.7%). This suggested that animals with milder (undetectable) pathology might also be capable of transmitting.

Previous work suggested that in the minority of badgers exhibiting severe pathology, 20% had kidney infections (Gallagher *et al.,* 1976).

Subsequent work detailed that renal lesions were the second most common type of gross lesion seen in these animals (Gallagher and Nelson, 1979). Independently, the ISG reported that the incidence of renal lesions in proactively and reactively culled badgers was 13% and 14.6% respectively. It should be noted however that the reported frequency of renal lesions is extremely variable between studies (Corner *et al.,* 2010). Urine from such infected badgers was reported to contain <300,000 bacilli per millilitre (MAFF, 1979), whilst in subsequent studies, up to 250,000 colony forming units per millilitre were found (Gallagher, 1998). Badgers urinate whilst walking; typically producing urine trails of more than 0.5 metres (Brown, 1993). It is conceivable that other badgers inspecting urine trails near territorial boundaries could somehow aerosolise and inhale bacilli and become infected. *M. bovis* in badger urine only survives for ~3 days on summer pasture and ~14 days on winter pasture (MAFF, 1979; Garnett *et al.,* 2002) due to the differing intensity of solar UV radiation, which can kill the bacilli.

Infected badgers may also shed *M. bovis* in faeces deposited at latrines close to territorial boundaries (Hutchings *et al.,* 2001). Bacilli in faeces are thought to originate from ingestion of respiratory mucus (Gallagher and Clifton-Hadley, 2000). Up to 75 colony forming units per gram of faeces have been observed (Gallagher, 1998). Again, this is a potential source of infection for other animals inspecting such sites. A number of studies in different countries indicate that the survival of *M. bovis* in environmental matrices is variable. *M. bovis* in faeces or faeces-contaminated soil appears to remain viable for up to ~6 months in some studies (Maddock, 1933; Saxer and Vanarburg, 1951; Courtenay *et al.,* 2006). The effect that differing soil temperature and humidity have on viability has yet to be fully elucidated (Phillips *et al.,* 2003). It is our opinion consequently, that the relative contribution of indirect transmission remains unknown. Current thinking, as in human TB epidemiology, would require the aerosolisation and inhalation of infectious particle with defined characteristics (small droplet nuclei) from these 'indirect' sources. It has been difficult to envisage how, or indeed where, this would happen in this system, although it is not inconceivable – see section 4, page 19.

Another potential route of infection for badgers, more commonly seen in males, is bite wounding (Clifton-Hadley *et al.,* 1993). The resulting pathology is significantly worse and is more localised in abdominal regions (Jenkins *et al.,* 2008b). Pus exuded from infected wounds may also be a source of *M. bovis* for transmission (Rogers *et al.,* 2000;

Phillips *et al.,* 2003). These studies suggest that infected badgers can, theoretically at least, excrete *M. bovis* in exhaled air, sputum, urine, faeces and pus (Phillips *et al.,* 2003): indeed bacilli have been isolated from the latter four matrices (Cheeseman *et al.,* 1985; Delahay *et al.,* 2006), suggesting potential routes and sources of infection for other wildlife and cattle. However, direct respiratory transmission is now considered the most likely transmission route between badgers themselves and between badgers and cattle (ISG, 2007).

Of the ~15% of tuberculous, culled badgers from the RBCT, 41.7% exhibited some form of pathology (Woodroffe *et al.,* 2009a). A minority (~7%) of these badgers had widespread severe lesions and generalised TB (Jenkins et al., 2008b; Woodroffe et al., 2009a). Previously, it had been suggested that relatively few terminally ill badgers, with severe pathology and high bacterial load, shed bacilli on a regular basis, the so-called 'super-excretor' (super-shedder or super-spreader), and they could potentially account for most transmission from badgers to cattle (Gallagher and Clifton-Hadley, 2000; Wilkinson *et al.,* 2000). However, RBCT data suggested that these may account for as little as 0.4% of all adult badgers (Jenkins *et al.,* 2008b) and consequently may not constitute a major source of infection.

It should also be noted that not all badgers with culture positive TB exhibit lesions detectable by standard *post mortem* protocols (ISG, 2007; Woodroffe *et al.,* 2009a). Indeed, this is the case for the majority of infected badgers. Previously, badgers with microscopic lesions were suggested to be controlling the infection and were therefore considered non-infectious (Gallagher et al., 1998). However, more recently, there is little evidence that this is the case (Jenkins et al., 2008b), leading to speculation that badgers exhibiting milder pathology and/or microscopic lesions in the lungs and kidneys may also be able to transmit infection, as above (ISG, 2007; Jenkins *et al.,* 2008b; Murphy *et al.,* 2010). The observation that infected cattle, with no gross visible lesions, could still excrete *M. bovis* intermittently (McCorry *et al.,* 2005) supports this hypothesis.

In summary, previously a variety of primarily indirect routes of transmission had been proposed to predominate. Whilst these routes may contribute to disease transmission, in recent years the debate has favoured direct contact and transmission of a principally respiratory infection.

4.2.3 Cattle-to-badger transmission.

One route of disease transmission to badgers is from infected cattle themselves. During the RBCT, proactive badger culling and cattle test-and-slaughter and movements were suspended temporarily in 2001 due to the outbreak of food and mouth disease in GB. Upon resumption of badger culling, it was observed that the prevalence of badger TB had increased (ISG, 2007). This was interpreted as evidence that infectious cattle, under movement standstill and not removed by test and slaughter, were also able to spread infection to wildlife. This increased TB prevalence was also observed in RTA badgers outside the RBCT (Woodroffe *et al.,* 2006). This illustrates that there can be a cycle of infection between species which needs to be interrupted effectively.

4.2.4 TB and badger ecology.

In undisturbed wild badger populations, TB appears to spread slowly and clusters patchily amongst a minority of individuals (Delahay *et al.,* 2000). Mortality due to TB within the population appears to depend on how well individuals deal with infection. Badgers able to control disease and prevent excretion of *M. bovis* do not exhibit increased mortality, whereas those which excrete and super-excrete do (Wilkinson *et al.,* 2000). Whilst TB has been reported as the most significant infectious cause of badger mortality, its effect on overall mortality is relatively low in comparison to road traffic accidents (Cheeseman *et al.,* 1988).

Rogers *et al* (1998) reported a correlation between new infections arising in different social groups and inter-group movement. It has been shown that such movement, into previously disease-free social groups, can be precipitated by the shrinking of group size and a relative increase in females, possibly brought on by the loss of males through natural causes or RTA (Vicente *et al.,* 2007). This would be supported by the observed behaviour of males from one group moving into another for opportunistic mating. Should these males be infected they may spread the infection to at least some of their new social group. The fact that males appear to exhibit increased susceptibility to infection and more rapid progression (Wilkinson *et al.,* 2000), as well as increased ranging when infected (Garnett *et al.,* 2005), will probably serve to enhance transmission. This phenomenon does appear to be quite rare in undisturbed populations with infected and uninfected social groups observed to co-exist with little evidence of disease transmission between them (Macdonald *et al.,* 2006). Such clustering of disease in badgers was also noted by the ISG (2007), supported by the findings of a recent study where badgers from various social groups were fitted with proximity data logging collars (Böhm *et al.,* 2009). This study indicated that inter-group contact in undisturbed populations was very rare.

Badger removal in ROI has been shown to disrupt the social structure of the population and to result in increased ranging (O'Corry-Crowe *et al.,* 1996). Whilst researchers in ROI do not report a corresponding perturbation-linked increase in cattle TB prevalence, the potential for cross infection may well be increased by such actions (Kelly *et al.,* 2010; O'Corry-Crowe *et al.,* 1996). Although not proven, heterogeneity of badger density may impact on badger movement and contacts in the ROI.

It is very difficult without definitive data to determine the exact relationship between badger density, badger movement, TB prevalence and potential cattle badger contact. All of these factors are likely to vary over space and time in different regions.

5 Interfaces of badger-to-cattle TB transmission.

As discussed previously, most of the current understanding of disease transmission derives from pathology studies in badgers and cattle and from ecology and epidemiology studies in badgers and cattle, respectively. The pathology observed in badgers and cattle indicates that TB is principally transmitted via infectious droplet nuclei in aerosols expelled intermittently from infectious cases.

The most likely route(s) of transmission between badgers and cattle have been inferred from pathological findings. In cattle, a considerably larger oral dose of bacilli is required to initiate infection than is required for respiratory infection (Morris *et al.,* 1994) indicating that cattle are more likely to be infected through inhalation rather than ingestion. Pathology findings from reactor cattle support this conclusion.

There remains the theoretical possibility that cattle inspecting infected badger urine/faeces may aerosolise bacilli, inhale them and establish infection. The epidemiology of other veterinary pathogens, for which the direct aerosol transmission route is accepted as the main route, involves infection by inhalation of aerosolised bacteria from environmental sources. For example *Coxiella burnetii,* the causative pathogen of Q Fever, has been observed to infect animals and humans exposed to contaminated wool (Angelakis and Raoult, 2010). Additionally, *Mycobacterium avium paratuberculosis*, the causative agent in Johne's Disease has been observed to be aerosolised in dust particles derived from bovine faecal material in animal housing (Eisenberg *et al.,* 2010).

Based on the pathology of infected cattle, the vast majority of TB is found in the respiratory tract suggesting that, again, infection in cattle is mostly caused by inhalation of bacilli (Phillips *et al*., 2003). It seems more likely therefore that badger-cattle transmission involves inhalation of aerosolised bacilli during close contact between animals. These direct or indirect routes of infection may occur either at pasture or in animal housing facilities.

5.1 Badger-to-cattle transmission at pasture.

5.1.1 Direct transmission via close contact.

Historically, direct contact between cattle and badgers at pasture was considered relatively infrequent and consequently of low risk (Ward *et al.,* 2010). Cattle which have been turned out to pasture after winter housing have been observed to exhibit an inquisitive nature and desire to investigate badgers (Benham and Broom, 1989; Ward *et al.,* 2010). However, when investigated, most badgers tended to avoid cattle (Benham, 1985).

Recent work (Böhm *et al.* 2009) suggests that whilst cattle–badger contact at pasture is infrequent, it may not be as infrequent as previously thought. Using data logging proximity collars fitted to both badgers and cattle, Böhm *et al* (2009) demonstrated that, over a six month period, five of thirteen collared cattle came into close proximity (1.5 to 2.5 metres) to collared badgers at pasture (Böhm *et al.,* 2009). The frequency of these inter-species contacts exceeded those of inter-social group contacts between badgers. Inter-species contact was also variable between different geographical locations, with some areas exhibiting a greater number of contacts of longer duration (Böhm *et al.,* 2009). This was typically a feature of areas in which highly territorial badger behaviour was observed. Cattle highest in the herd hierarchy exhibited the greatest level of contact with badgers and the greatest level of contact with other herd members (Böhm *et al.,* 2009).

This illustrates their potential role as hubs for disease transmission. The potential for direct respiratory transmission of *M. bovis* in the field between species may be a greater risk than previously thought.

Other work has indicated that badgers infected with *M. bovis* exhibit aberrant behaviour, including increased ranging (Garnett *et al.,* 2005) and a reduced aversion to contact with cattle (Cheeseman and Mallinson, 1981). These behaviours may also serve to increase contact between cattle and infected badgers. Badgers found dead or *in extremis* in farmyards were also three times more likely to be infected with TB than those killed in RTAs (Cheeseman and Mallinson, 1981). This may be further evidence of the altered behaviour of infected badgers, which includes wider ranging and possibly a higher tendency to seek more readily-available food sources. In some extreme examples Muirhead *et al.* (1974) reported that one ailing badger was found living above ground in a pig sty, whilst another was observed to fearlessly approach humans on farm in broad daylight.

5.1.2 Indirect transmission via excreta/exudates.

The previously accepted primacy of indirect transmission routes derives from earlier studies. For example, Muirhead *et al.,* (1974) suggested that contamination of pasture with infected badger excreta or sputum may be the primary source of indirect infection for cattle. Indirect transmission assumed precedence over direct, close contact transmission between species because it was believed that cattle and badgers mostly avoided each other (Hutchings and Harris, 1999; Ward *et al.,* 2010) and cattle mostly avoided badger faeces when grazing (Benham, 1985). Indeed Griffin *et al.* (1992) suggested that contaminated faeces are less likely to be a source of infection than urine for cattle. Similarly, cattle appeared to avoid consuming badger urine-contaminated herbage for up to fourteen days, if given the choice (Benham and Broom, 1991).

A hierarchy exists within cattle herds. Subordinate cattle tended to graze closer to badger urine trails and latrines. In cases of heavy stocking density, when there is increased competition for better sward, even high ranking animals were forced into such behaviour (Hutchings and Harris, 1997). In cases of reduced stocking density, where cattle have more choice regarding the grass they consume, contamination by badger urine and faeces may still be a potential source of infection. Some cattle, whilst not grazing on such contaminated grass, investigated it by sniffing (Benham and Broom, 1991).

Cows tended to graze grass at the edges of fields with a general overuse of herbage at perimeter fences (Hutchings and Harris, 1997; Phillips, 1993), grazing areas coincidentally co-localise with those areas that badgers were most likely to use for territorial marking with urine and/or faeces (see 3.1). This cattle behaviour may increase potential exposure to contaminated excreta. This is a risk only if cattle can be infected via the indirect route. Considering that cattle and badgers are more likely to contemporaneously occupy pasture during the spring and summer months, it seems likely that potential infection of cattle is probably a balance between bacterial persistence and the degree of aversion cattle feel towards grazing contaminated sward (Phillips *et al.,* 2003), the latter being influenced by competition for sward.

If cattle are fed at pasture or provided with licks, badger access to these food sources may enhance sputum/salivary-based transmission risks (Ward *et al.,* 2010). Feeding at pasture may generally enhance risks of transmission since badgers have been shown to have a fondness for various types of cattle feed/concentrates and 'cake' (Garnett *et al.,* 2003; Tolhurst *et al.,* 2009). Badgers have been observed to use feed troughs on pasture as both a source of food and also as latrines, potentially leading to further indirect exposure of cattle to pathogen (Garnett *et al.,* 2003).

Another potential source of infection may arise when cattle come into contact with badger setts in woodland neighbouring pasture or in hedgerows (Ward *et al.,* 2010). Cattle have been observed to 'head rub' at setts and investigate discarded bedding which may contain bacilli from sputum, pus or other exudates (Phillips *et al.,* 2003). Again, however, current opinion is converging on the predominance of the direct contact/respiratory route for disease transmission, within and between species.

5.2 Badger-to-cattle transmission in cattle housing.

5.2.1 Badger visits to farms and potential for close contact and indirect transmission.

Although less common than visitations to feed stores, badger visits to cattle housing have also been recorded (Tolhurst *et al.,* 2009).

Therefore, direct contact between cattle and badgers in farm buildings is a potential and possibly important source of transmission. Badgers have been observed in video surveillance to eat food from the same troughs as cattle and at the same time (Garnett *et al.,* 2002; Roper *et al.,* 2003). An additional reason for visiting animal housing may be to collect straw for sett bedding (Garnett *et al.,* 2002; Roper *et al.,* 2003). In such visits, the proximity between the two species can be as little as two metres (Garnett *et al.,* 2002), providing ample opportunity for inhalation of aerosolised bacteria from infectious cases.

Badger visitations to farm buildings have been noted previously (MAFF, 1979; MAFF, 1981; Benham, 1985; Kruuk and Parish, 1985; Ward *et al.,* 2008a). Philips *et al.* (2003) proposed two reasons why UK farms may be attractive to badgers; the storage of high energy foods in accessible places and availability of new maize varieties nutritious to wildlife (Philips *et al.,* 2003). It has been shown that badgers visited feed stores (Garnett *et al.,* 2002; Tolhurst, 2006) and exhibited a preference for cattle 'cake' /concentrates over all other food types (Tolhurst *et al.,* 2009). Visits to maize and silage clamps have also been observed in video surveillance of buildings (Ward *et al., 2010*). As successful opportunists and scavengers, it is not surprising that badgers have been observed to leave their normal habitat and adapt to, and take advantage of, all available food sources (Mullineaux, 2003).

Several studies have attempted to quantify badger visits to farmyards and farm buildings. Radio tracking, video and camera surveillance studies on farm revealed that visits could occur on up to 50% of nights investigated (Ward *et al.,* 2010). Subsequent surveys in the south west of England uncovered signs of badger visitation in 39% of studied farms (Ward *et al.,* 2008a). Interestingly, several studies have indicated that badger visitations peak in the summer months, in times of dry weather (Ward *et al.,* 2008a) perhaps as a result of reduced earthworm activity, which is normally greatest after rainfall (Kruuk and Parish, 1981; Garnett *et al.,* 2002). Badger ranges also tended to begin to overlap with farm buildings in spring and summer (Tolhurst *et al.,* 2009). Badger visits to farm buildings were shown to be negatively correlated to rainfall (Garnett *et al.,* 2002). It seems likely that at dry times of the year, when their major food source is scarce or unavailable, it may be attractive for badgers to visit farm buildings to consume readily-available cattle feed (Garnett *et al.,* 2002).

Tolhurst *et al.* (2009) demonstrated by radio-tracking that badger visits to feed stores were more common than visits to any other type of farm building, including animal housing, farmyards and silage clamps. These findings suggest that the main purpose of farm visits is to find food. Badgers have been observed to urinate and defecate on or near to stored cattle feed (Garnett *et al.,* 2002) in what has been proposed to be territorial marking of a food source (Revilla and Palomares, 2002). Both urine and faeces are potential sources of indirect infection, along with other exudates like sputum, saliva and pus. The presence of any of these substances on cattle feed may constitute a risk of indirect infection (Garnett *et al.,* 2002). Such indirect transmission between another wildlife species, white tailed deer, and cattle via indirect contamination of feedstuffs, has been demonstrated in Michigan, USA (Palmer *et al.,* 2004).

Work conducted in the ROI (Sleeman *et al.,* 2008) reported that 1.4% of 200 herds surveyed exhibited signs of badger visitation (ie. badger tracks) in winter months when cattle were housed indoors. However, the robustness of these findings has been challenged since GB camera-based surveillance showed that badger visitations did not always lead to visible signs, such as tracks. Reliance on such signs may underestimate the true prevalence of visitations by ~33% (Judge *et al.,* 2009). They also suggested that a better picture of badger visitation would be gained in the summer months, since this behaviour was highly seasonal (Judge *et al.,* 2009).

5.3 Management actions to mitigate transmission.

Based on the current understanding of disease source(s) and spread, derived largely from pathological findings, pragmatic management actions (other than the strategic deployment of effective badger vaccination, badger culling, badger fertility control etc.), which could reasonably be predicted to reduce the probability of disease transmission, are discussed. Comprehensive badger population and ecological / behavioural data exist in GB, leading to the communication of generic advice to herd-keepers on how best to manage and minimise the risks posed at the badger-cattle interface. It has not yet been possible to produce a ranked list of interventions or to prescribe mitigations on a farm-by-farm basis.

5.3.1 Management actions to mitigate transmission at pasture.

There are potential strategies, summarised in Table 1 (after Ward *et al* 2010), which could further reduce the probability of infectious contacts (direct or indirect) at the badger-cattle interface.

Moving cattle between grazed areas more regularly could reduce direct contact (Ward *et al.,* 2010) as well as letting the sward grow longer in rotated pasture. Longer grass is believed to discourage badger foraging for earthworms since they prefer shorter sward where worms are easier to catch at the surface (Kruuk *et al.,* 1979). Additionally, some authors suggest deliberately keeping some pasture near active setts short and not grazing it as a means to prevent contact (Ward *et al.,* 2010). This may also be a viable means of restricting badger activity to un-grazed sward and thereby preventing or reducing direct contact between species.

Husbandry practices were suggested by the Independent Husbandry Panel (IHP), set up by the then Ministry of Agriculture, Forestry and Fisheries, MAFF (Phillips *et al.,* 2000). The IHP made particular reference to the impact that different grazing regimes may have on the likelihood of cattle being exposed (indirect) to infectious materials at pasture. Set stocking of a fixed number of cattle over one area of pasture for a long time was particularly discouraged, especially if it involved high cattle densities. Such stocking can reduce the sward length more than with other regimes (Phillips, 2002). When sward was reduced it encouraged badger foraging, increased excretion of potentially infectious urine and faeces and also less selective grazing or reduced aversion to badger excreta in cattle (Ward *et al.,* 2010; Hutchings and Harris, 1997). Again, rotational grazing regimes may help minimise contact with potentially infectious excreta (Phillips, 2001).

Another strategy may be to prevent cattle from grazing at the edges of fields which are likely to be badger territorial boundaries and consequently a repository for territorial marking with urine and faeces. Applying a strip grazing regime, in which the perimeters of any pasture land are fenced off with electric fencing, thereby retaining cattle on the strip of land less likely to be affected by urine and faecal contamination, may achieve the latter (Ward *et al.,* 2010). Similarly, fencing off badger setts may be an effective way of reducing contact with discarded bedding material and excreta, and potentially direct contact with badgers (Ward *et al.,* 2010). In cases where farmers do not have a large number of separate land parcels, reduction of stocking density per available field may also help to reduce overgrazing and the potential of exposure to contaminated sward (Hutchings and Harris, 1997; Phillips *et al.,* 2000; Gallagher *et al.,* 2003). All of the above grazing regimes should reduce the potential risks of exposure to contaminated pasture, but some cattle, regardless of the measures discussed, will still consume grass on or near badger excreta (Hutchings and Harris, 1997).

It may also be beneficial to manipulate the times at which potential exposure might occur. Badgers are largely nocturnal, so any deposition of urine or faeces at pasture is likely to occur at night. It has been proposed that the infection risks posed by urine/faeces deposited on pasture by night should have diminished substantially by the following afternoon, especially if exposed to germicidal UV light (King, 1997) and it would be a precaution to delay introduction of cattle to such high risk pasture until later in the day (Ward *et al.,* 2010).

It has been recommended to avoid providing supplementary feed to cattle at pasture, particularly in the case of pasture close to badger setts (Phillips *et al.,* 2000). Raising the height of feeding and water troughs to prevent or reduce badger access has also been recommended and is included in the DEFRA advice to farmers (DEFRA Animal Health, 2010a). This approach may however not be fully effective as badgers are known to be exceptional climbers (Neal and Cheeseman, 1996; Mullineaux, 2003), with studies showing that raising troughs to 80 centimetres above ground is insufficient to completely exclude all badger access (Garnett *et al.,* 2003). Some (but importantly not all) badgers were able to climb to 115 centimetres above ground (Garnett *et al.,* 2003). This may still be an effective means of reducing indirect contact between badgers and cattle.

5.4 Management actions to mitigate transmission in farm buildings.

The most obvious way to prevent either direct or indirect contact between badgers and cattle in farm buildings is to prevent badger entry. DEFRA advises excluding badger access to farm buildings, which can be effectively achieved in a variety of practical, physical bio-security measures, including making sure all buildings are secure at night, gates etc are closed and no gaps or holes are present in doors or walls through which wildlife can gain access (DEFRA Animal

Health, 2010b). Similarly, farmers should install solid, sheer doors/gates on buildings to prevent badger access by climbing over or through them (DEFRA Animal Health, 2010b). Also, farmers are advised to ensure that gaps between the bottom of gates/doors and the ground are no more than ten centimetres (DEFRA Animal Health, 2010b). Such measures can dramatically reduce badger access to farm yards (Central Science Laboratory, 2009). However, recent surveys demonstrate that only 14% of TB-affected farmers in England have adopted such bio-security measures (Ward *et al.,* 2010; Bennet and Cooke, 2005).

A further option for deterring badger entry to farm buildings is electric fencing. Fences specifically designed to exclude badgers have been used very effectively to prevent/reduce damage to crops (Poole *et al.,* 2002). Use of this specific fence system on farm has also resulted in effective exclusion of badgers from farm buildings in DEFRA trials and other independent studies (Central Science Laboratory, 2006; Tolhurst *et al.,* 2008; Central Science Laboratory, 2009). DEFRA recommend using electric fences with wires set at 10, 15, 20 and 30 centimetres above the ground to ensure effectiveness (DEFRA Animal Health, 2010b).

Tolhurst *et al.* (2008) demonstrated that badgers exposed to electric fencing exhibited aversion behaviour resulting in reduced challenges to the fences once they had been in place for some time. As a means of encouraging contact between badgers and the fences and thereby enhancing aversion rates, they recommended attaching novel objects to the fencing that badgers would inspect. Electric fences should be installed over concrete thereby preventing badgers from digging under them, as seen with non-electrified fences (Poole *et al.,* 2002). Keeping fences in place throughout the most high risk season may be the most sensible approach as normal foraging behaviour was observed to resume six weeks after fence removal (Poole *et al.,* 2004). Tolhurst et al. (2008) observed that the exclusion of badgers from farm buildings had an ecological effect on the badger populations. They tended to range further, presumably as a result of having to forage more for food. However, this increased ranging did not involve encroaching on other badger social group territories and is therefore not analogous to the danger of cull-induced perturbation and disease spread between social groups.

Whilst complete exclusion from buildings may negate the need to further prevent access to foodstuffs on farm, DEFRA advise that it may be desirable to implement additional measures. Use of secure, solid storage bins for foods with lids which can be fixed in place or locked is desirable (DEFRA Animal Health, 2010b). Badgers are excellent climbers, and are more agile and more resourceful than would be appreciated in accessing food stores (Garnett *et al.,* 2002; Central Science Laboratory, 2006). Also, covering the face of silage clamps to prevent badger access should be encouraged (DEFRA Animal Health, 2010b). Ensuring that cattle are fed only in secure housing is essential, as is cleaning up of any spillages of feed which may attract wildlife (DEFRA, Animal Health, 2010a; DEFRA, Animal Health, 2010b). Several authors suggest that feeding troughs need to be re-designed to prevent or minimise badger access (Garnett *et al.,* 2003; Ward *et al.,* 2010). However, provided access to the housing in which animals are fed can be prevented, this is perhaps less of an issue than troughs at pasture.

More technically-advanced means of reducing badger access to farmyards could include the use of motion sensor-equipped water jets or ultrasonic devices. However, recent trials have not been as successful as the more practical measures discussed above (Ward *et al.,* 2008b). In particular, ultrasonic devices actually attracted badgers to food sources and water jets had only a small beneficial effect in deterring badger access to buildings. Overall, the more practical and easier to implement improvement of existing farm bio-security, alongside installation of improved gates, fences and electric fences is recommended to exclude badgers from farm buildings. Recent DEFRA data indicates that the average cost to farmers to improve bio-security is ~£4,000. Considering the average cost of dealing with a TB herd breakdown in GB (~£27,000), these measures would appear to be a cost-effective way of attempting to reduce potential TB transmission between species (Central Science Laboratory, 2009).

A summary of the potential husbandry measures to reduce transmission at both pasture and at housing is shown in Table 1 below (after Ward *et al* 2010).

	Recommendations	Rationale
At pasture	Use a rotational grazing system	Promotes herding, decreases familiarity and increases potential for badgers to avoid cattle.
	Fence off setts and latrines.	Reduces potential for contact with badger excretory products.
	Do not graze pasture too short.	Reduces potential for contact with badgers and their excretory products.
	Avoid field margins when cutting silage.	Reduces potential for contact with badger excretory products.
	Do not introduce cattle to recently cut fields.	Reduces potential for contact with badger excretory products.
In farmyards	Move cattle to fresh pasture in the afternoon.	Reduces potential for contact with badger excretory products.
	Do not provide supplementary feeding on pasture.	Reduces potential for badgers to contaminate feed.
Both	Keep buildings/doors/gates well maintained.	Reduces potential for badgers to come into contact with cattle.
	Close doors and bottom sheet gates.	Reduces potential for badgers to contaminate feed.
	Store feed in closed bins/secure buildings.	Reduces potential for badgers to contaminate feed.
	Do not feed cattle on the ground.	Reduces potential for badgers to contaminate feed.
	Protect stored feed with electric fences at night.	Reduces potential for badgers to contaminate feed.
	Repair damaged walls, fences and gates.	Reduces potential for badgers to contaminate feed.
	Place feed blocks and mineral licks in a container raised off the ground.	Reduces potential for badgers to contaminate feed.
	Design troughs to prevent badger access.	

Table 1: Recommendations and rationale for mitigating steps which should reduce the risk of badger-cattle transmission (after Ward *et al* 2010)

5.4.1 General – field and farm.

Bio-security advice to farmers should also make them aware of the dangers of unlicensed badger and sett disturbance. GB and ROI researchers have indicated that badger removal, especially if not performed in a structured, efficient manner, can result in the disruption of badger social structure and potentially increase infectious contacts and risks to local cattle herds (Woodroffe *et al.,* 2009a; O'Corry-Crowe *et al.,*1996; Kelly *et al.,* 2010). In the absence of definitive local evidence and supporting ecological data, perturbation by badger persecution / sett disturbance should still be viewed as a potential risk in NI.

While not specifically part of this review, it is also worth noting that intra-muscular vaccination of badgers with Bacillus Calmette Guérin (BCG) has been observed to reduce the severity and progression of experimental TB infection in captive badgers and the frequency of *M. bovis* isolation from clinical samples (Chambers *et al.,* 2010). Vaccination may have an important role to play in managing the risk of direct disease transmission from badgers to cattle.

6 Conclusions.

6.1 Badger/cattle interfaces most likely to lead to TB transmission.

The extent to which infectious badgers contribute to TB in cattle remains un-quantified and indeed may be un-quantifiable. The evidence suggests that respiratory transmission is the main route of infection in both badgers and cattle. Transmission by direct, close contact appears to be more important than transmission via indirect contact. Badgers and cattle appear to have more direct contact than previously envisaged.

There is a lack of quantitative data on which transmission routes and settings are pre-eminent. It is impossible to provide a definitive ranked list of interventions which would be likely to reduce cattle and badger contact and thereby reduce the probability of transmission. Local variations in badger ecology and density across different geographic areas appear to have varying effects on badger ranging behaviour, and consequently a potential effect on infectious badger-cattle contacts.

It would be beneficial to undertake a province-wide survey in which badger populations, ecology and behaviour and their effects on badger–cattle contact at pasture or in animal housing could be assessed. Making use of telemetry and/or data logging cattle and badger collars could determine primary badger – cattle interfaces and their variation.

We have been unable to provide definitive risk and intervention rankings. However, we agree with Ward *et al* (2010) that some basic steps could be taken to help to try to reduce cattle–badger contact. We recommend improving farm bio-security, with an emphasis on preventing direct badger–cattle contact ie:

- Ensure all buildings (animal housing, feed stores, silage clamps etc) are secured at night.
- Close all gates and doors.
- Fill all gaps and holes in doors, walls, gates and fences.
- Install solid, sheer doors/gates to prevent badger access.
- Ensure that gaps between the bottom of doors/gates and the ground are <10 centimetres.
- Install electric fencing (ideally over concrete) with four wires set at 10, 15, 20 and 30cm above the ground.
- Use secure food storage bins.
- Do not leave food uncovered or on the floor of buildings. Clean up all spillages.
- Elevate food and water troughs to 80 centimetres above the ground.

Importantly, effective engagement with farmers (affected and unaffected) will be essential to the success of any future scheme to improve bio-security. Going forward, it is important to optimise and improve the way bio-security information is disseminated, so that farmers can make informed decisions about the measures needed. Currently many farmers may be unaware of the risks and the steps they could reasonably take to reduce the potential risk from badgers.

7 References

Abernethy, D.A., Walton, E., Menzies, F., Courcier, E., Robinson, P. (2010). *Mycobacterium bovis* surveillance in European badgers (*Meles meles*) killed by vehicles in Northern Ireland: an epidemiological evaluation. International Conference on Animal Health Surveillance, Lyon, France, 2011.

Angelakis, E. and Raoult, D. (2010). Q Fever. *Veterinary Microbiology* **140**, 297-309.

Benham, P.F.J. (1985). The behaviour of badgers and cattle and some factors that affect the chance of contact between the species. *Applied Animal Behaviour Science* **14**, 390-391.

Benham, P.F.J. and Broom, D.M. (1989). Interactions between cattle and badgers at pasture with reference to bovine TB transmission. *British Veterinary Journal* **145**, 226-241.

Benham, P.F.J. and Broom, D.M. (1991). Responses of dairy cows to badger urine and faeces on pasture with reference to bovine TB transmission. *British Veterinary Journal* **147**, 571-532.

Böhm, M., Hutchings, M.R., White, P.C.L. (2009). Contact networks in a wildlife-livestock host community: Identifying high risk individuals in the transmission of bovine TB among badgers and cattle. *PLoS One* **4**, e5016.

Bouvier, G., Burgisser, H. and Schneider, P.A. (1957). *Schweizer Arch. Tierheil.* **99**, 461.

Brown, J.A. (1993). Transmission of bovine TB (*Mycobacterium bovis*) from badgers (*Meles meles*) to cattle. *Ph.D., University of Bristol.*

Carpenter, P.J., Pope, L.C. and Greig, C. (2005). Mating system of the Eurasian badger, *Meles meles*, in a high density population. *Molecular Ecology* **14**, 273-284.

Central Science Laboratory (2006). An investigation of potential badger / cattle interactions including the extent of badger visitations to farm buildings and food stores, and how cattle husbandry methods may limit these. *Final Project Report SE3029* DEFRA London.

Central Science Laboratory (2009). An experiment to assess the cost effectiveness of farm husbandry manipulations to reduce risks associated with farmyard contact between badgers and cattle. *Final Project Report SE3119* DEFRA London.

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., Carter, S., Cheeseman, C., Hanks, C., Murray, A., Palphramand, K., Pietraville, S., Smith, G.C., Tomlinson, A., Walker, N.J., Wilson, G.J., Corner, L.A.L., Rushton, S.P., Shirley, M.D.F., Gettinby, G., McDonald, R.A., Hewinson, R.G. (2010). Bacillus Calmette-Guérin vaccination reduces the severity of TB in badgers. *Proceedings of the Royal Society B* doi:10.1098/rspb.2010.1953

Cheeseman, C.L. and Mallinson, P.J. (1981). Behaviour of badgers (*Meles meles*) infected with bovine TB. *Journal of Zoology* **194**, 284-289.

Cheeseman, C.L., Little, T.W.A., Mallinson, P.J., Rees, W.A., Wilesmith, J.W. (1985). The progression of bovine TB infection in a population of *Meles meles* in south-west England. *Acta Zool. Fenn.* **173**, 197-199.

Cheeseman, C.L., Wilesmith, J.W., Stuart, F.H., Mallinson, P.J. (1988). Dynamics of TB in a naturally infected badger population. *Mammal Review* **18**, 61-72.

Clarke, G.P., White, P.C.L., Harris, S. (1998). Effects of roads on badger *Meles meles* populations in south-west England. *Biological Conservation* **86**(2), 117-124.

Cleary, G., Corner, L., O'Keefe, J., Marples, N.M. (2009). The diet of the badger *Meles meles* in the Republic of Ireland. *Mammalian Biology* **74**, 438-447.

Clements, E.D., Neal, E. and Yalden, D.W. (1988). The national badger sett survey. *Mammal Review* **18**, 1-19.

Clifton-Hadley, R.S., Wilesmith, J.W., Stuart, F.A. (1993). *Mycobacterium bovis* in the European badger (*Meles meles*): epidemiological findings in tuberculous badgers from a naturally infected population. *Epidemiology and Infection* **111**, 9-19.

Corner LA, Costello E, Lesellier S, O'Meara D, Sleeman DP, Gormley E. Experimental TB in the European badger (*Meles meles*) after endobronchial inoculation of Mycobacterium bovis: I. Pathology and bacteriology. *Res Vet Sci.* 2007 Aug;**83**(1):53-62. Epub 2007 Jan 2. PubMed PMID: 17197004.

Corner, L.A.L., Clegg, T.A., More, S.J., Williams, D.H., O'Boyle, I., Costello, E., Sleeman, D.P. and Griffin, J.M. (2008). The effect of varying levels of population control on the prevalence of TB in badgers in Ireland. *Research in Veterinary Science* **85**, 238-249.

Corner LA, Costello E, Lesellier S, O'Meara D, Gormley E. Experimental TB in the European badger (Meles meles) after endobronchial inoculation with Mycobacterium bovis: II. Progression of infection. *Res Vet Sci.* 2008 Dec;**85**(3):481-90. Epub 2008 Apr 22. PubMed PMID: 18433810.

Corner, L.A.L., Murphy, D. and Gormley, E. (2010). *Mycobacterium bovis* infection in the Eurasian badger (*Meles meles*): the disease, pathogenesis, epidemiology and control. *Journal of Comparative Pathology* (epub ahead of print).

Costello, E., Flynn, O., Quigley, F., O'Grady, D., Griffin, J., Clegg, T., McGrath, G. (2006). Genotyping of *Mycobacterium bovis* isolates from badgers in four areas of the Republic of Ireland by restriction fragment length polymorphism analysis. *Veterinary Record* **159**, 619-623.

Courtenay, O., Reilly, L.A., Sweeney, F.P., Hibberd, V., Bryan, S., Ul-Hassan, A., Newman, C., Macdonald, D.W., Delahay, R.J., Wilson, G.J., Wellington, E.M.H. (2006). Is *Mycobacterium bovis* in the environment important for the persistence of bovine TB. *Biology Letters* **2**, 460-462.

Cranshaw, T.R., Griffiths, I.B., Clifton-Hadley, R.S. (2008). Comparison of a standard and a detailed post-mortem protocol for detecting *Mycobacterium bovis* in badgers. *Veterinary Record* **163**, 473-477.

Cresswell, W.J., Harris, S. (1988). Foraging behaviour and home range utilization in a suburban badger (*Meles meles*) population. *Mammal Review* **18**, 37-49.

Cresswell, P., Harris, S. and Jefferies, D.J. (1990). The history, distribution, status and habitat requirements of the badger in Britain. *Nature Conservancy Council, Peterborough.*

DAFF (1996). Badger Manual. Department of Agriculture Food and Forestry (DAFF), Dublin, Ireland, p 37.

DANI Report (1978). Annual report on Research and Technical Work 1978. *Department of Agriculture for Northern Ireland, Belfast, HMSO,* p170.

DARD (2008). Badger Survey of Northern Ireland 2007/2008. http://www.dardni.gov.uk/badger-survey-of-ni-2007-08.pdf

DEFRA Animal Health (2010a). Dealing with TB in your herd – How to reduce the risk of bovine TB (TB) on your premises. *Advice and Guidance* **9**.

DEFRA Animal Health (2010b). Dealing with TB in your herd – Understanding the risk of bovine TB (TB) to cattle from wildlife. *Advice and Guidance* **10**.

Delahay, R.J., Langton, S., Smith, G., Clifton-Hadley, R.S. (2000). The spatio-temporal distribution of *Mycobacterium bovis* (bovine TB) infection in a high density badger population. *Journal of Animal Ecology* **69**, 428-441.

Delahay, R.J., Wilson, G., Rogers, L.M., Cheeseman, C.L. (2003). TB and the badger: culling as a method to control a wildlife disease reservoir. In: Tattersall, F.H., Manley, W.J. (Eds), Conservation and Conflict: Mammals and farming in Britain. Linnaean Society Occasional Publication Series, Smith Settle, Otley, pp165-171.

Delahay, R.J., Smith, G.C., Ward, A.I., Cheeseman, C.L. (2006). Options for the management of bovine TB transmission from badger (*Meles meles*) to cattle: evidence from a long term study. *Mammal Study* **30**, S73-S81.

Denny, G.O. and Wilesmith, J.W. (1999). Bovine TB in Northern Ireland: a case control study of herd risk factors. *Veterinary Record* **144**, 305-310.

Donnelly, C.A., Woodroffe, R., Cox, D.R., Bourne, J., Gettinby, G., Le Fevre, A.M., McInerney, J.P. and Morrison, W.I. (2003). Impact of localised badger culling on TB incidence in British cattle. *Nature* **426**, 834-837.

Donnelly, C.A., Wei, G., Johnston, W.T., Cox, D.R., Woodroffe, R., Bourne, F.J. *et al.* (2007). Impacts of widespread badger culling on cattle TB: concluding analyses from a large scale field trial. *International Journal of Infectious Disease* **11**, 300-308.

Drewe, J.A., Tomlinson, A.J., Walker, N.J., Delahay, R.J. (2010). Diagnostic accuracy and optimal use of three tests for TB in live badgers. *PLoS One* 5, e11196.

Durr, P.A., Hewinson, R.G. & Clifton Hadley, R.S. (2000). Molecular epidemiology of bovine TB. *Mycobacterium bovis* genotyping. *Rev. Sci. Tech.* **19**, 675-688

Eisenberg, S.W.F., Nielen, M., Santema, W., Houwers, D.J., Heederik, D., Koets, A.P. (2010). Detection of spatial and temporal spread of *Mycobacterium avium* subsp. *pararTB* in the environment of a cattle farm through bio-aerosols. *Veterinary Microbiology* **143**, 284-292.

Eves, J.A. (1999). Impact of badger removal on bovine TB in east County Offaly. *Irish Veterinary Journal* **52**, 199-203.

Feore, S.M. (1994). The distribution and abundance of the badger, *Meles meles L.* in Northern Ireland. Unpublished PhD thesis. Queen's University Belfast, UK.

Feore, S.M., Montgomery, W.I. (1999). Habitat effects on the spatial ecology of the European badger (*Meles meles*) *Journal of Zoology* (Lond) **247**, 537-549.

Gagneux, S. and Small, P.M. (2007). Global phylogeography of *Mycobacterium TB* and implications for TB product development. *Lancet Infectious Diseases* **7**, 328-337.

Gallagher, J., Muirhead, R.H., Burn, K.J. (1976). TB in wild badgers (*Meles meles*) in Gloucestershire, pathology. *Veterinary Record* **98**, 9-14.

Gallagher, J.and Nelson, J. (1979). Causes of ill health and natural death in badgers in Gloucestershire. *Veterinary Record* **105**, 546-551.

Gallagher, J. (1998). The natural history of spontaneous TB in wild badgers. *Doctor of Veterinary Medicine Thesis,* University of London.

Gallagher, J., Monies, R., Gavier-Widen, M., Rule, B. (1998). Role of infected, non-diseased badgers in the pathogenesis of TB in the badger. *Veterinary Record* **142**, 710-714.

Gallagher, J. and Clifton-Hadley, R.S. (2000). TB in badgers: A review of the disease and its significance for other animals. *Research in Veterinary Science* **69**, 203-217.

Gallagher, E., Kelly, L., Pfeiffer, D.U., Wooldridge, M. (2003). A quantitative risk assessment for badger to cattle transmission of *Mycobacterium bovis*. *Proceedings of the Society of Veterinary Epidemiology and Preventative Medicine* 33-44.

Garnett, B.T., Delahay,R.J., Roper, T.J., (2002). Use of cattle farm resources by badgers (*Meles meles*) and risk of bovine TB (*Mycobacterium bovis*) transmission to cattle. *Proceedings of the Royal Society B* **269**, 1487-1491.

Garnett, B.T., Roper, T.J., Delahay, R.J. (2003). Use of cattle troughs by badgers (*Meles meles*). A potential route for the transmission of bovine TB (*Mycobacterium bovis*) to cattle. *Applied Animal Behaviour Science* **80**, 1-8.

Garnett, B.T., Delahay, R.J., Roper, T.J. (2005). Ranging behaviour of European badgers (*Meles meles)* in relation to bovine TB (*Mycobacterium bovis*) infection. *Applied Animal Behaviour Science* **94**, 331-340.

Griffin, J.M., Hahesy, T., Lynch, K. (1992). The role of farm management practices and environmental factors in chronic TB. *Irish Veterinary Journal* **45**, 120-122.

Griffin, J.M., Williams, D.H., Kelly, G.E., Clegg, T.A., O'Boyle, I., Collins, J.D. and More, S.J. (2005). The impact of badger removal on the control of TB in cattle herds in Ireland. *Preventive Veterinary Medicine* **67**, 237-266.

Hutchings, M.R. and Harris, S. (1997). Effects of farm management practices on cattle grazing behaviour and the potential for transmission of bovine TB from badgers to cattle. *Veterinary Journal* **153**, 149-162.

Hutchings, M.R. and Harris, S. (1999). Quantifying the risks of TB infection to cattle posed by badger excreta. *Epidemiology and Infection* **122**, 167-174.

Hutchings, M.R., Service, K.M., Harris, S. (2001). Defecation and urination patterns of badgers *Meles meles* at low density in south west England. *Acta Theriologica* **46**, 87-96.

Hutchings, M.R., Service, K.M., Harris, S. (2002). Is population density correlated with faecal and urine scent marking in European badgers (*Meles meles*) in the UK? *Mammalian Biology* **67**, 286-293.

ISG (1999). An epidemiological investigation into bovine TB: towards a sustainable policy to control TB in cattle, Second report of the Independent Scientific Group on Cattle TB, MAFF Publications, London.

ISG (2007). Bovine TB: The Scientific Evidence. A science base for a sustainable policy to control TB in cattle. Final report of the Independent Scientific Group on Cattle TB, DEFRA Publications, London.

Jenkins, H.E., Woodroffe, R., Donnelly, C.A. (2008a). The effects of annual widespread badger culls on cattle TB following the cessation of culling. *International Journal of Infectious Diseases* **12**, 457-465.

Jenkins, H.E., Morrison, W.I., Cox, D.R., Donnelly, C.A., Johnston, W.T., Bourne, F.J., Clifton-Hadley, R.S., Gettinby, G., McInerney, J.P., Watkins, G.H., Woodroffe, R. (2008b). The prevalence, distribution and severity of detectable pathological lesions in badgers naturally infected with *Mycobacterium bovis*. *Epidemiology and Infection* **136**, 1350-1361.

Jenkins, H.E., Woodroffe, R., Donnelly, C.A. (2010). The duration of the effects of repeated widespread badger culling on cattle TB following the cessation of culling. *PLoS One* **5**, issue 2, e9090. http://www.plosone.org/annotation/listThread.action?inReplyTo=info%3Adoi%2F10.1371%2Fannotation%2F2444ce5c-b56d-4ea3-a554-ffba25152c66&root=info%3Adoi%2F10.1371%2Fannotation%2F2444ce5c-b56d-4ea3-a554-ffba25152c66

Judge, J., Ward, A., Delahay, R., MacDonald, R., Roper, T., Tolhurst, B., Ben Garnett. (2009). Tracking badger visits to farmyards. *The Veterinary Record* **164**, 667.

Kelly, G.E., Condon, J., More, S.J., Dolan, L., Higgins, I. and Eves, J. (2008). A long term observational study of the impact of badger removal on herd restrictions due to bovine TB in the Irish midlands during 1989-2004. *Epidemiology and Infection* **136**, 1362-1373.

Kelly, G.E., More, S.J. (2010). Spatial clustering of TB infected cattle herds prior to and following proactive badger removal. *Epidemiology and Infection* doi:10.1017/S0950268810002323.

Kelly, G.E., McGrath, G.E., More, S.J. (2010). Estimating the extent of spatial association of *Mycobacterium bovis* infection in badgers in Ireland. *Epidemiology and Infection* **138**, 270-279.

King, E. (1997). Factors influencing the risks to cattle of infection with bovine TB (*Mycobacterium bovis*) from badgers (*Meles meles*). Ph.D. Thesis, University of Bristol.

Krebs, J.R. (1997). Bovine TB in cattle and badgers. Report to the Rt Hon Dr Jack Cunningham MP, Ministry of Agriculture, Fisheries and Food, London.

Kruuk, H., Parish, T., Brown, C.A.J., Carrera, J. (1979). The use of pasture by the European badger (*Meles meles*). *Journal of Applied Ecology* **16**, 453-459.

Kruuk, H. and Parish, T. (1981). Feeding specialisation of the badger (*Meles meles*) in Scotland. *Journal of Animal Ecology* **50**, 773-788.

Kruuk, H. and Parish, T. (1982). Factors affecting population density, group size and territory size of the European badger (*Meles meles*). *Journal of Zoology* **196**, 31-39.
Kruuk, H. and Parish, T. (1985). Food, food availability and weight of badgers *(Meles meles)* in relation to agricultural changes. *Journal of Applied Ecology* **22**, 705-715.

Little, T.W.A., Naylor, P.F. and Wilesmith, J.W. (1982). Laboratory study of *Mycobacterium bovis* infection in badgers and calves. *Veterinary Record* **111**, 550-557.

McCorry, T., Whelan, A.O., Welsh, M.D., McNair, J., Walton, E., Bryson, D.G., Hewinson, R.G., Vordermeier, H.M., Pollock, J.M. (2005). Shedding of *Mycobacterium bovis* in the nasal mucus of cattle infected experimentally with TB by the intranasal and intratracheal routes. *Veterinary Record* **157**, 613-618.

Macdonald, D.W. and Newman, C. (2002). Population dynamics of badgers (*Meles meles*) in Oxfordshire, UK: numbers, density and cohort life histories, and a possible role of climate change in population growth. *Journal of Zoology London* **256**, 121-138.

Macdonald, D.W., Harmsen, B.J., Johnson, P.J., Newman, C. (2004). Increasing frequency of bite wounds with increasing population density in Eurasian badgers, *Meles meles. Animal Behaviour* **67**, 745-751.

Macdonald, D.W., Riordan, P., Mathews, F. (2006). Biological hurdles to the control of TB in cattle: A test of two hypotheses concerning wildlife to explain the failure of control. *Biological Conservation* **131**, 268-286.

Maddock, E.C.G. (1933). Studies on the survival time of the bovine TB bacillus in soil, soil and dung, in dung and on grass, with experiments on the preliminary treatment of infected organic matter and the cultivation of the orgasnism. *Journal of Hygiene* **33**, 103-117.

MAFF Report (1976). Bovine TB in badgers. *Ministry of Agriculture, Fisheries and Food, London.*

MAFF Report (1977). Bovine TB in badgers. *Second report by Ministry of Agriculture, Fisheries and Food, London.*

MAFF Report (1979). Bovine TB in badgers. *Third report by Ministry of Agriculture, Fisheries and Food, London.*

MAFF Report (1981). Bovine TB in badgers. *Fifth report by Ministry of Agriculture, Fisheries and Food, London.*

Menzies, F.,D., Abernethy, D.A., Stringer, L.A., Jordan, C. (2011). A comparison of badger activity in two areas of high and low bovine TB incidence of Northern Ireland. *Veterinary Microbiology* **151**, 112-119.

Morris, R.S., Pfeiffer, D.U., Jackson, R. (1994). The epidemiology of *Mycobacterium bovis* infections. *Veterinary Microbiology* **40**, 153-177.

Muirhead, R.H., Gallagher, J. and Burn, K.J. (1974). TB in wild badgers in Gloucestershire: epidemiology. *Veterinary Record* **95**, 552.

Mullineaux, E. (2003) Badgers. In BSAVA Manual of Wildlife Casualties. Eds E. Mullineaux, D. Best, J. E. Cooper. British Small Animal Veterinary Association pp 123-136.]

Murphy, D., Gormley, E., Costello, E., O'Meara, D., Corner, L.A.L. (2010). The prevalence and distribution of *Mycobacterium bovis* infection in European badgers (*Meles meles)* as determined by enhanced post mortem examination and bacteriological culture. *Research in Veterinary Science* **88**, 1-5.

Murphy, D., Gormley, E., Collins, D.M., McGrath, G., Sovsic, E., Costello, E., Corner, L.A.L. (2011). TB in cattle herds are sentinels for *Mycobacterium bovis* infection in European badgers (*Meles meles*): The Irish Greenfield Study. *Veterinary Microbiology* **151**, 120-125.

Neal, E.G. (1988). The stomach contents of badgers. *Journal of Zoology* (London) **215**, 367-369.

Neal, E.G. and Cheeseman, C. (1996). Badgers. Poyser Natural History.

Noonan, N.L., Sheane, W.D., Harper, L.R. and Ryan, P.J. (1975). *Irish Veterinary Journal* **29**, 1.

O'Connor, C.M., Haydon, D.T., Kao, R.R. (2009). Great Britain and Republic of Ireland badger culling trials: An initial comparative study. *SVEPM Conference Proceedings 2009.* http://www.bovinetb.info/docs/Connor.pdf

O'Corry-Crowe, G., Eves, J., Hayden, T.J.F. (1993). Sett distribution, territory size and population density of badgers (*Meles meles* L.) in east Offaly. In: Hayden TJ (ed) The badger. Royal Irish Academy, Dublin, pp35-56.

O'Corry-Crowe, G., Hammond, R., Eves, J., Hayden, T.J. (1996). The effect of reduction in badger density on the spatial organisation and activity of badgers *Meles meles* L. in relation to farms in central Ireland. *Biology and Environment Proceedings of the Royal Irish Academy* **96B**, 147-158.

Olea-Popelka, F.J., Flynn, O., Costello, E., McGrath, G., Collins, J.D., O'Keeffe, J., Kelton, D.F., Berke, O., Martin, S.W. (2005). Spatial relationship between *Mycobacterium bovis* strains in cattle and badgers in four areas in Ireland. *Preventive Veterinary Medicine* **71**, 57-70.

Olea-Popelka, F.J., Phelan, J., White, P.W., McGrath, G., Collins, J.D., O'Keeffe, J., Duggan, M., Collins, D.M., Kelton, D.F., Berke, O., More, S.J., Martin, S.W. (2006). Quantifying badger exposure and the risk of bovine TB for cattle herds in county Kilkenny, Ireland. *Preventive Veterinary Medicine* **75**, 34-46.

Palmer, M.V., Waters, W.P., Whipple, D.L. (2004). Investigation of the transmission of *Mycobacterium bovis* from deer to cattle through indirect contact. *American Journal of Veterinary Research* **65**, 1483-1489.

Phillips, C.J.C. (1993). Cattle behaviour. Ipswich: Farming Press.

Phillips, C.J.C, Foster, C., Morris, P., Teverson, R. (2000). The role of cattle husbandry in the development of a sustainable policy to control *M. bovis* infection in cattle. Report of the Independent Husbandry Panel, May 2000, MAFF, London.

Phillips, C.J.C. (2001). Principles of cattle production. CABI Publishing, Wallingford.

Philips, C.J.C. (2002). Cattle behaviour and welfare, second edition. Blackwell Publishing, Oxford.

Phillips, C.J.C, Foster, C.R.W., Morris, P.A., Teverson, R. (2003). The transmission of *Mycobacterium bovis* infection to cattle. *Research in Veterinary Science* **74**, 1-15.

Poole, D.W., McKillop, I.G., Western, G., Hancocks, P.J., Packer, J.J. (2002). Effectiveness of an electric fence to reduce badger (*Meles meles*) damage to field crops. *Crop Protection* **21**, 409-417.

Poole, D.W., Western, G., McKillop, I.G. (2004). The effects of fence voltage and the type of conducting wire on the efficacy of an electric fence to exclude badgers (*Meles meles*). *Crop Protection* **23**, 27-33.

Reid, N., Etherington, T.R., Wilson, G., McDonald, R.A. and Montgomery, W.I. (2008). Badger survey of Northern Ireland 2007/2008. Report prepared by Quercus and Central Science Laboratory for the Department of Agriculture and Rural Development (DARD), Northern Ireland, UK.

Revilla, E. and Palomares, F. (2001). Differences in key habitat use between dominant and subordinate animals: intraterritorial dominance payoffs in Eurasian badgers? *Canadian Journal of Zoology* **79**, 165-170.

Rogers, L.M., Delahay, R., Cheesman, C.L., Langton, S., Smith, G.C., Clifton-Hadley, R.S. (1998). Movement of badgers (*Meles meles*) in a high density population: individual population and disease effects. *Proceedings of the Royal Society of London B* **265**, 1269-1276.

Rogers, L.M., Delahay, R.J., Hounsome, T.D., Cheeseman, C.L. (2000). Changes in badger (*Meles meles*) spatial organisation in Woodchester Park, south west England. *In: Griffiths, H. (Ed.), Mustelids in the Modern World.* Hull University Press, Hull.

Roper, T.J., Garnett, B.T., Delahay, R.J. (2003). Visits to farm buildings and cattle troughs by badgers (*Meles meles*): a potential route for transmission of bovine TB (*Mycobacterium bovis*) between badgers and cattle. *Cattle Prac.* **11**, 9-12.

Saxer, E. and Vanarburg, H. (1951). Untersuchungen uber die Lebensfahigkeit von tuberkelbazillen (Investigations concerning the viability of tubercule bacilli). *Pathologie und Bakteriologie* **14**, 532-536.

SGM – Society for General Microbiology (2008). www.defra.gov.uk/animalh/tb/pdf/report-oct2008.pdf

SGM - Society for General Microbiology (2009). The DEFRA commissioned independent review of bovine TB research. *Microbiology Today* February 2009, 33-35.

Skuce, R.A. *et al.* (2005). Discrimination of isolates of *Mycobacterium bovis* in Northern Ireland on the basis of variable numbers of tandem repeats (VNTRs). *Veterinary Record* **157**, 501-504.

Skuce, R.A., Mallon, T.R., McCormick, C.M., McBride, S.H., Clarke, G., Thompson, A., Couzens, C., Gordon, A.W., McDowell, S.W.J. *Mycobacterium bovis* genotypes in Northern Ireland: herd-level surveillance (2003-2008).

Sleeman, D.P. (1992). Long distance movements in an Irish badger population. In: Priede I.G., Swift S.M. (eds) Wildlife telemetry. Ellis Horwood, Chichester, pp670-676.

Sleeman, D.P., Mulcahy, M.F. (2005). Loss of territoriality in a local badger *Meles* meles population at Kilmurry, Co. Cork, Ireland. *Ir. Nat. Journal* **28**, 11-19.

Sleeman, D.P., Davenport, J., Fitzgeraldm A. (2008). Incidence of visits by badgers to farmyards in Ireland in winter. *Veterinary Record* **163**, 724.

Sleeman, D.P., Davenport, J., More, S.J., Clegg, T.A., Collins, J.D., Martin, S.W., Williams, D.H., Griffin, J.M., O'Boyle, I. (2009). How many Eurasian badgers *Meles meles* L. are there in the Republic of Ireland? *European Journal of Wildlife Research* **55**, 333-344.

Smal (1995). The badger and habitat survey. Government Publications Dublin.

Smith, N.H., Dale, J, Inwald, J., Palmer, S., Gordon, S.V., Hewinson, R.G., Smith, J.M. (2003). The population structure of *Mycobacteriuym bovis* in Great Britain: clonal expansion. *Proceedings of the National Academy of Sciences of the United States of America* **100**, 15271-15275.

Smith, N.H., Gordon, S.V., De la Rua Domenech, R., Clifton-Hadley, R.S., Hewinson, R.G. (2006). Bottlenecks and Broomsticks: The molecular evolution of *Mycobacterium bovis. Nature Reviews Microbiology* **4**, 670-681.

Tolhurst, B.A. (2006). Behaviour of badgers (*Meles meles*) in farm buildings, in relation to the transmission of bovine TB (*Mycobacterium bovis*) between badgers and cattle, Unpublished Ph.D thesis, University of Sussex.

Tolhurst, B.A., Ward, A.I., Delahay, R.J., MacMaster, A.M., Roper, T.J. (2008). The behavioural responses of badgers (*Meles meles*) to exclusion from farm buildings using an electric fence. *Applied Animal Behaviour Science* **113**, 224-235.

Tolhurst, B.A., Delahay, R.J., Walker, N.J., Ward, A.I., Roper, T.J. (2009). Behaviour of badgers (*Meles meles*) in farm buildings: opportunities for the transmission of *Mycobacterium bovis* to cattle. *Applied Animal Behaviour Science* **117**, 103-113.

Tuyttens, F.A.M., MacDonald, D.W., Rogers, L.M., Cheeseman, C.L., Roddam, A.W. (2000). Comparative study on the consequences of culling badgers (*Meles meles*) on biometrics, population dynamics and movement. *Journal of Animal Ecology* **69**, 567-580.

Vial, F., Donnelly, CA (2011). Localized reactive badger culling increases risk of bovine TB in nearby cattle herds. *Biol Lett.* Epub ahead of print.

Vial, F., Johnston, W.T., Donnelly, C.A. (2011). Local cattle and badger populations affect the risk of confirmed TB in British cattle herds. *PLoS One* **6,** e18058.

Vicente, J., Delahay, R.J., Walker, N.J., Cheeseman, C.L. (2007). Social organisation and movement influence the incidence of bovine TB in an undisturbed high density badger *Meles meles* population. *Journal of Animal Ecology* **76**, 348-360.

Ward, A.I., Tolhurst, B.A., Walker, N.J., Roper, T.J., Delahay, R.J. (2008a). A survey of badger access to farm buildings and facilities in relation to contact with cattle. *Veterinary Record* **163**, 107-111.

Ward, A.I., Pietravalle, S., Cowan, D.P., Delahay, R.J. (2008b). Deterrent or dinner bell? Alteration of badger activity and feeding at baited plots using ultrasonic and water jet devices. *Applied Animal Behaviour Science* **115**, 221-232.

Ward, A.I., Judge, J. and Delahay, R.J. (2010). Farm husbandry and badger behaviour: Opportunities to manage badger to cattle transmission of *Mycobacterium bovis*? *Preventive Veterinary Medicine* **93**, 2-10.

White, P.C.L. and Harris, S. (1995). Bovine TB in badgers (*Meles meles*) populations in Southwest England – an assessment of past, present, and possible future control strategies using simulation modelling. *Philos Trans R Soc Lond B Biol Sci* **264**, 1737-1747.

Wilson, G., Harris, S. and McLaren G. (1997). Changes to the British badger population, 1988-1997. *People's trust for endangered species, London.*

Wilkinson, D., Smith, G.C., Delahay, R.J., Rogers, L.M., Cheeseman, C.L., Clifton-Hadley, R.S. (2000). The effects of bovine TB (*Mycobacterium bovis*) on mortality in a badger (*Meles meles*) population in England. *Journal of Zoology London* **250**, 389-395.

Woodroffe, R., Macdonald, D.W. and da Silva, J. (1993). Dispersal and philopatry in the Eurasian badger, *Meles meles*. *Journal of Zoology* **237**, 227-239.

Woodroffe, R., Donnelly, C.A., Johnston, W.T., Bourne, F.J., Cheeseman, C.L., Clifton-Hadley, R.S., Cox, D.R., Gettinby, G., Hewinson, R.G., Le Fevre, A.M., McInerney, J.P., Morrison, W.I. (2005). Spatial association of *Mycobacterium bovis* infection in cattle and badgers *Meles meles. Journal of Applied Ecology* **42**, 852-862.

Woodroffe, R., Donnelly, C.A., Jenkins, H.E., Johnston, W.T., Cox, D.R., Bourne, F.J., Cheeseman, C.L., Delahay, R.J., Clifton-Hadley, R.S., Gettinby, G., Gilks, P., Hewinson, R.G., McInerney, J.P., Morrison, W.I. (2006). Culling and cattle controls influence TB risk for badgers. *Proceedings of the National Academy of the Sciences (USA)* **103**, 14713-14717.

Woodroffe, R., Donnelly, C.A., Cox, D.R., Gilks, P., Jenkins, H.E., Johnston, W.T., Le Fevre, A.M., Bourne, F.J., Cheeseman, C.L., Clifton-Hadley, R.S., Gettinby, G., Hewinson, R.G., McInerney, J.P., Mitchell, A.P., Morrison, W.I., Watkins, G.H. (2009a). Bovine TB in cattle and badgers in localised culling areas. *Journal of Wildlife Diseases* **45**, 128-143.

Woodroffe, R. Donnelly, C.A., Wei, G., Cox, D.R., Bourne, F.J., Burke, T., Butlin, R.K., Cheeseman, C.L., Gettinby, G., Gilks, P., Hedges, S., Jenkins, H.E., Johnston, W.T., McIerney, J.P., Morrison, W.I., Pope, L.C. (2009b). Social group size affects *Mycobacterium bovis* infection in European badgers (*Meles meles*). *Journal of Animal Ecology* **78**, 818-827.