

# Control of bovine tuberculosis in British livestock: there is no 'silver bullet'

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**Bovine tuberculosis (bTB; *Mycobacterium bovis*) is a bacterial infection of cattle that also affects certain wildlife species. Culling badgers (*Meles meles*), the principal wildlife host, results in perturbation of the badger population and an increased level of disease in cattle. Therefore, the priority for future management must be to minimize the risk of disease transmission by finding new ways to reduce the contact rate among the host community. At the farm level, targeting those individuals that represent an elevated risk of transmission might prove to be effective. At the landscape level, risk mapping can provide the basis for targeted surveillance of the host community. Here, we review the current evidence for bTB persistence in Britain and make recommendations for future management and research.**

## Wildlife hosts for bovine tuberculosis

Many infections of humans and their livestock are able to cross-infect multiple host species [1]. The presence of infections within a multiple-host community can complicate attempts to reduce disease [2,3], not only because of varying resistance to infection between the different host species but also because of ecological and behavioural differences.

Bovine tuberculosis (bTB; *Mycobacterium bovis*) persists in various countries in the developed world. In some of these countries (including Britain, Ireland and New Zealand), the presence of additional wildlife hosts for the infection – principally Eurasian badgers (*Meles meles*) in the UK and Ireland, and brush-tailed possums (*Trichosurus vulpecula*) and ferrets (*Mustela putorius*) in New Zealand – is thought to have contributed to the persistence of the disease in cattle, despite considerable investment in culling programmes to reduce the populations of these wildlife hosts. Badgers are particularly well suited as a host for bTB because they are a group-living animal. They exhibit a range of social structures, with social group size varying between two individuals in Poland and 25 individuals in Britain, and group territories ranging from 0.14 km<sup>2</sup> in Britain to 14 km<sup>2</sup> in Poland and Finland [4].

In Britain, the total economic costs associated with bTB between 2004 and 2011 are expected to reach £1 billion [5]. A test-and-slaughter strategy to detect and remove bTB-infected cattle from British herds had all but

eradicated bovine bTB in a large part of Britain by the 1970s, and persistent infection was limited to distinct areas in southwest Britain. Since that time, badgers have been implicated increasingly in the persistence and re-emergence of bTB as the disease has spread once more into new areas, both within southwest Britain and beyond.

A large-scale field trial, the Randomized Badger Culling Trial (RBCT), was initiated in 1999 to determine the extent of badger involvement in bTB in cattle and the effectiveness of culling badgers in reducing bTB infection in cattle [6,7]. The field trial showed that badger culling over 100-km<sup>2</sup> areas could result in a decrease in cattle bTB inside these areas, with effectiveness increasing with distance from the boundary, but that bTB in cattle increased in areas immediately surrounding the culled area [8]. Based on these results, members of the Independent Scientific Group (ISG), which coordinated the trial, concluded that badger culling could not contribute meaningfully to the control of cattle bTB in Britain [9,10]. Subsequently, others have questioned the conclusions of the ISG [11]. The UK government's scientific advisor, Sir David King, has proposed that badger culling should continue to be considered as a means of bTB control (<http://www.defra.gov.uk/animalh/tb/pdf/badgersreport-king.pdf>), and the Welsh Assembly Government has announced that it intends to resume badger culling (<http://new.wales.gov.uk/news/presreleasearchive/2131604/?lang=en>).

## To cull or not to cull: the spectre of perturbation

One of the reasons that the interpretation of the RBCT results by the ISG has been questioned is the evidence from Ireland, where intensive culling of badgers has led to reductions in bTB in cattle across large areas [12]. The increase in bTB in the areas immediately surrounding the culling areas in the RBCT has been attributed to the disturbance to the social system of the badgers after culling; this disturbance is commonly referred to as 'perturbation' [13]. Badgers living at moderate-to-high densities (>5 badgers per km<sup>2</sup>) in undisturbed populations concentrate their urinations and defecations at specific sites known as latrines [4], but the lower population densities that result from culling can lead to a more dispersed pattern of scent marking. This might increase the risk of transmission of any bTB infection to cattle because grazing cattle show reduced avoidance behaviour of single faeces relative to established latrine sites [14,15].

However, the true effect of culling goes beyond simply reducing numbers. After culling at intermediate levels, the normally well-established territorial systems of badgers can become disrupted by the increased immigration of badgers into culled areas. This increased movement has been linked with elevated levels of bTB in badger populations [16]. Territorial behaviour of badgers in undisturbed populations tends to be ritualized, and levels of aggression between badgers of neighbouring groups are kept low through neighbour recognition, whereby the ability to distinguish familiar individuals from strangers encourages reduced aggression between holders of neighbouring territories (the ‘dear enemy’ effect [17]). However, increased levels of aggression are shown towards dispersing or itinerant (alien) badgers [18], so when populations are perturbed, general levels of aggression – and, hence, opportunities for bTB transmission – will increase.

In contrast to Britain, there is no evidence for any such perturbation effects in Ireland after intensive badger control. One likely contributory reason for this is the existence of natural geographical barriers to dispersal (i.e. the coastline and major rivers) around the culled areas in Ireland [12]. Other possible reasons include variations in the prevalence of bTB in the existing badger populations, variations in the area of land over which badgers have been controlled and the efficiency of control [10]. Levels of bTB prevalence in badger populations are quite consistent between Britain and Ireland, but there are substantial differences in the areas over which badgers have been controlled in the two countries and the efficiency with which this has been done. In Ireland, badger culling is currently being carried out proactively over areas ranging in size between 188 and 305 km<sup>2</sup> with the overall policy aim of maintaining badger populations at <20% of their original densities over 30% of the area of agricultural land, which is equivalent to a 25–30% overall reduction in the national badger population (J. O’Keeffe, personal communication). In Britain during the RBCT, badgers were culled using cage traps in ten separate 100-km<sup>2</sup> areas, and trapping efficiency for the initial culling period was estimated at 71–85% in seven areas, and 35–46% in three areas [19]. The use of restraints (snares) in Ireland enables a high efficiency of badger culling, which is likely to minimize problems caused by perturbation, but animal-welfare-based legislation prohibits the use of restraints to catch badgers in Britain. Independently developed strategic disease models have indicated that the reduction of bTB in badger populations requires a badger-culling efficiency of at least 80–90% [20–22]. These original estimates have been reinforced by the differences in control efficacy experienced in Britain and Ireland, and they correspond with other estimates of the efficiencies required from one-off culling operations for the control of related bacterial diseases in mammalian hosts [23]. The efficiency of the use of restraints by experienced field staff in Ireland can approach these levels, whereas to achieve such high levels of badger removal over large areas using cage trapping alone would require a huge investment in time and resources and, even if it were achievable, it

would be extremely unlikely to yield any net economic benefits [10]. Moreover, the current UK Government considers such widespread badger culling to be politically and socially unacceptable [10].

#### **Local-scale behavioural processes: interactions and contact networks**

The results from the RBCT have been valuable in improving our knowledge of the link between badgers, cattle and cattle bTB. Nevertheless, the statistical models that have been developed to relate bTB in cattle to various host, environmental and climatic variables are characterized by a poor fit [24–27]. A considerable proportion of the variation in cattle bTB, therefore, remains unexplained, but the clumped distribution of the disease implies that local spatial processes are likely to be important and account for up to 75% of the variation in bTB outbreaks in high-risk areas [27]. Unfortunately, because these models are characterized by poor or missing data on badger distribution and abundance, the statistical contribution of badgers remains unclear.

From the management perspective, the characteristics of neighbouring areas help to determine the cattle bTB-testing intervals to be applied in specific areas and, from the epidemiological perspective, opportunities for infection via local contact networks will determine the persistence of disease in an area. Genotyping work on *M. bovis*, which has demonstrated the clumped distribution of distinct genetic strains and the sharing of the same strains among different species in the same spatial areas, has provided further indirect evidence of the existence of inter-species transmission networks [28]. Potential pathways in the transmission network include direct contact between cattle (including spread between contiguous properties), direct contact among badger populations or between badgers and cattle, and indirect contact between the species that occurs via the contamination of pasture with faeces and urine. However, genotyping can reveal only limited information on the directionality of transmission within such networks [29] so, despite their potential significance, the nature of these contact networks remains elusive.

An improved understanding of the local-scale behavioural processes underlying transmission events is likely to provide valuable insights into the nature of these networks and, therefore, into management that could reduce the frequency of contact between hosts and, hence, reduce the rate of transmission events. Studies have shown that direct contact between badgers and cattle can occur in farm buildings and at feeding troughs [30,31] and that cattle can also come into contact with badger excretory products at latrines and crossing-points (i.e. where badgers might urinate or defecate after passing through hedgerows) [32]. However, detailed studies of potential transmission events via direct contact among individuals within badger populations or between badgers and cattle on pasture have been restricted until recently to visual observations [33], which inevitably account for only a small proportion of the contact during an individual’s activity period. Therefore, for nocturnal, group-living

animals such as badgers, much contact activity has remained unknown.

Recent advances in biotelemetry resulting in the development of proximity data-logging devices have opened up new opportunities for detailed studies of animal-interaction patterns. These devices have already revealed highly heterogeneous contact networks within populations of wildlife and domestic animals, including possums, raccoons and cattle [34–36], and they are now being applied to the study of contact between badgers and cattle. Analysis of radio-tracking data obtained simultaneously from different neighbouring individual badgers has shown that, although badgers forage independently, individuals within the same social group associate with one another more closely and, hence, make more contact with one another than would be expected by chance [37]. Moreover, badger social groups comprise different coalitions that are based on differential sett-use patterns and exhibit different levels of interactive behaviour [37] (Box 1). This is likely to lead to a heterogeneous contact structure within a population, which will affect the way in which diseases are transmitted through a social network. A similarly wide variation in behaviour for cattle has also been observed in other studies [36]. Using these data loggers on possums in New Zealand, Ji *et al.* [34] showed that relationships between contact rates and population density can be non-linear, which is likely to have contributed to the failure of one-off possum culling operations to control bTB in New Zealand (Box 2). Assessment of these contact networks within British livestock–wildlife–host systems across a range of densities is likely to reveal complex patterns of bTB transmission between hosts and emphasises the need for more process-based, rather than population-level, modelling. Moreover, such individual-based field approaches are essential if we are to develop effective, targeted control management based around certain high-risk subgroups within the population, which is likely to represent a more effective option for reducing disease than untargeted mass control does [38].

### **Spread of bTB across landscapes and within ecosystems**

Over the past ten years, bTB has spread from the southwest of England (which has, historically, been its geographical focus) to parts of England and Wales that have been unaffected by the disease since its eradication from large parts of the country in the 1960s [26,39]. Cattle movements have been shown to be the predominant contributory factor to the irruption of bTB in areas outside traditional disease hot spots [26,40], but the continued persistence of the disease in these new areas depends on the existence of a suitable host community.

Bovine TB has been found in a range of rodent, carnivore and ungulate species, but models indicate that it is unlikely that most of these species could act as true reservoirs of bTB infection [41]. However, there is a generally higher risk and uncertainty associated with bTB levels in deer, including roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and muntjac (*Muntiacus reevesi*) [42]. Deer have been implicated as a wildlife source for bTB in other parts of

the world [43–46], so bTB infection in the British farmland ecosystem could also be assisted by the presence of deer within the host community in certain areas. However, an assessment of the potential additional risk from deer is reliant on knowledge of the spatial distribution and abundance of the principal wildlife host, the badger, which has generally been the limiting factor in landscape-scale analyses of bTB incidence [24–26,47]. Significant associations between bTB persistence and badger-sett density have now been found at the farm scale [48] and recently published, improved models of badger abundance [49] now enable the association between bTB in cattle and badger density to be explored with greater confidence.

Risk maps based on the distribution of known or suspected hosts and vectors can be a valuable tool for disease management [50,51], in particular in relation to the identification of potential high-risk areas where introduced disease might establish in the host community. The increasing British deer population [52] means that the size and diversity of the potential bTB host community is also expanding in certain areas. In standard approaches to modelling the spread of contact-transmitted infections, which are based on the principle of mass action or frequency-dependent transmission [53,54], the number of new cases arising per unit of time is proportional to the density of susceptible and infectious hosts. The closest approximations to this type of theoretical disease transmission occur for highly transmissible infections that are transmitted between freely mixing hosts, but for many vertebrates, especially territorial species such as badgers, the assumptions of mass action are far removed from reality. Moreover, differences in disease behaviour relative to mass-action-type models are greatest when contact patterns are most heterogeneous and disease prevalence is low [55]. The simplified approach of mass-action-type models, therefore, has considerable shortcomings when applied in a tactical way for bTB in specific locations. Nevertheless, these models are still useful in a strategic sense, for example when making predictions of disease spread over large spatial areas, especially where empirical data on patterns of transmission are lacking. For the bTB disease system at the landscape level, therefore, it is reasonable to assume that single- or multiple-species guilds of potential hosts at higher densities are more likely to support bTB infection. Based on this assumption, a simple multiplicative relationship between the relative abundance scores of each of the potential bTB host groups (cattle, badgers and deer) can be used to indicate the relative capacity of the host community in different areas to maintain bTB and, hence, constitute a persistent risk to cattle (Box 3 and Figure 1).

This synthesis of existing datasets on host distributions highlights the existence of a substantial risk of bTB persistence in livestock–wildlife host communities in existing bTB hot spots, but it also highlights other areas, hitherto unaffected by bTB, where the infection has a higher chance of gaining a persistent foothold in the host community if introduced. The hypothetical disease risk posed by cattle and badgers (Figure 1a) is highest in traditional bTB ‘hot-spot’ areas such as the southwest of

Britain and southwest Wales and Cheshire, with high risk values also obtained in Cumbria, southwest and northeast Scotland and central North Yorkshire. The disease risk posed by cattle and deer combined (Figure 1b) is highest in southwest Britain, the southern Midlands (including the Cotswolds), central North Yorkshire, Cumbria, and southwest and northeast Scotland. Some of these areas coincide with the badger hot spots, although there are additional high-risk areas identified in parts of Scotland. The disease risk posed by the full potential host community (cattle, badgers and deer) reflects both of these distributions, with the highest overall risk areas in southwest Britain, the southern Midlands, Cumbria, North Yorkshire, and southwest and northeast Scotland (Figure 1c).

For a disease such as bTB, which has proven so difficult to eradicate once it becomes established in the wider ecosystem, it is imperative that there is greater surveillance in areas where the host community presents a higher risk of disease persistence so that any infection can be tackled before it becomes widespread in the ecosystem. Risk maps, such as those in Figure 1, can be used to direct surveillance efforts, which should be a priority for disease control [27] and are essential for developing a strategy with a more proactive, rather than reactive, approach to disease control. These basic risk maps could be enhanced considerably by improved data on bTB locations and wildlife population distribution, combined with more sophisticated spatial statistical modelling of risk.

### **Concluding remarks and future perspectives**

The management of bTB remains a controversial problem in Britain, which is made all the more intractable by the high number of factors that are actually or potentially contributing to its persistence in certain areas. To manage the disease more effectively, we need to understand the potential role of all these factors, including any synergistic effects. We also need to recognize that their relative importance is likely to vary between different areas because of differences in host-community composition and abundance, husbandry practices, landscape factors [56] and climatic conditions, which might affect the survival of bacilli in the environment [57].

Vaccination might provide some assistance in the control of bTB in host communities in Britain in the future [58,59], but this as yet untested approach should not be seen as the answer to the bTB problem. Although a badger vaccine might well contribute considerably to our ability to control bTB in the future, history has taught us that there are no 'silver bullets' when it comes to bTB eradication. Despite bTB being one of the best-studied disease systems in Britain, it is clear that there is still much to understand. Given this uncertainty, when developing bTB control strategies (e.g. through the use of epidemiological modelling frameworks), we should not assume levels of precision that are not supported by the available data. In particular, we should be wary of predictions based on mean field approaches when new research is increasingly showing us just how significant heterogeneity can be, from individual behaviour to landscape-level patterns of

transmission risk. A systems-based approach that builds on a mechanistic understanding of behaviour within all components of the system and considers all the control options seems to be a pragmatic starting point. This will require the cooperation of all stakeholders to ensure that bTB risk is managed at all levels – from farm management practices to bTB-testing regimes, livestock movements and wildlife-host-population reduction.

Based on the scientific evidence and means of management available at present, our recommendations are as follows:

(i) Traditional bTB hot-spot areas are characterized by rich host communities and, similarly, rich host communities exist in other areas that are, as yet, unaffected by bTB. Preventing bTB spreading to these areas must be a priority. The transport of cattle increases the risk of bTB spreading to new areas, so greater restrictions on cattle trade in these areas should be considered. In these high-risk areas, surveillance of the host community needs to be increased to reduce the likelihood of any introduced bTB becoming established in the wildlife community there. Investing in this surveillance now will reduce the likelihood of future (and potentially far more significant) costs because of bTB occurrence. It is imperative that this host-community surveillance is complemented by improvements to the cattle bTB-testing regime to minimize cattle-to-cattle transmission and spread after the seeding of infection into the wildlife host community by cattle (e.g. increased frequency of cattle bTB testing in high-risk areas outside of the current bTB distribution).

(ii) Proactive badger culling should not be completely discounted, and it might be the most appropriate technique for specific, spatially distinct bTB hot spots, such as newly emerging centres of disease where infection is not yet widespread among the surrounding host community. However, if carried out, it must not be selective, the efficiency must be high, and it must be done in conjunction with a range of cattle-based control methods. The effects of badger culling on badger population size and badger bTB prevalence should always be monitored and related to cattle bTB prevalence, and any badger-culling operation should be evidence-based with well-defined end points relating to expected disease-control targets.

(iii) There needs to be a focus on minimizing the reproductive capacity of the disease by reducing opportunities for transmission between hosts in all parts of the disease system. This should be done through a twin-level approach, based on the continued development of strategic assessments of risk at the landscape level alongside tactical approaches to reduce the opportunities for transmission at the farm level. The strategy for achieving this must be flexible according to the background conditions of disease and the host community in different local areas, and needs to be adaptive to changing conditions. In particular, greater effort should be put into understanding the links between these different levels in terms of how local contact processes contribute to disease persistence at the landscape level, and how and

why their relative importance changes in different situations.

(iv) BTB-control strategies should include changes to husbandry and farm management practices (e.g. fencing off cattle from concentrated areas of environmental contamination, such as latrines, and preventing access of wildlife to farm-stored food stuffs). The reduction of deer populations should also be considered, but it would be preferable to do this on the basis of more compelling evidence of the risks of bTB posed by deer to livestock. Management to reduce the risk of transmission needs to be applied by farmers in a collaborative manner so that it is applied consistently over wide areas of the landscape.

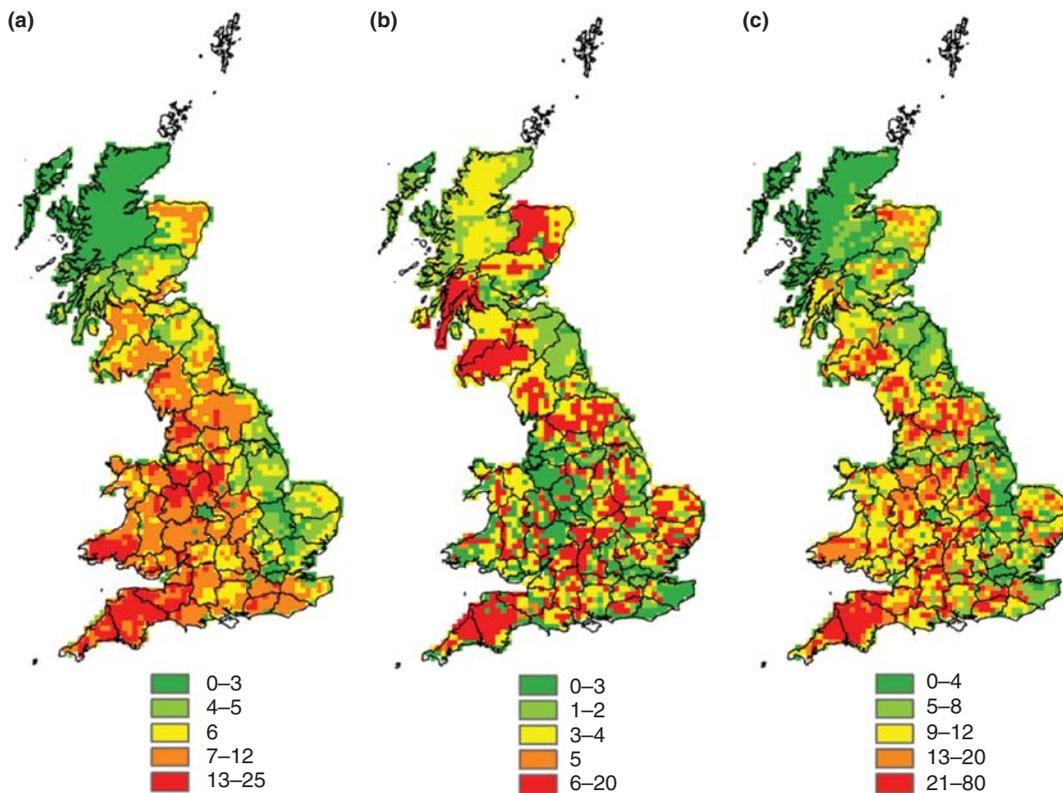
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TRENDS in Microbiology

**Figure 1.** Maps of Britain showing hypothetical risk scores for bTB persistence in the host community per 10-km square based on (a) cattle and badgers, (b) cattle and deer, and (c) cattle, badgers and deer combined. See Box 3 for details of methods. Lower risk areas are identified by green shading, and higher risk areas are identified by red shading. County boundaries are also shown.

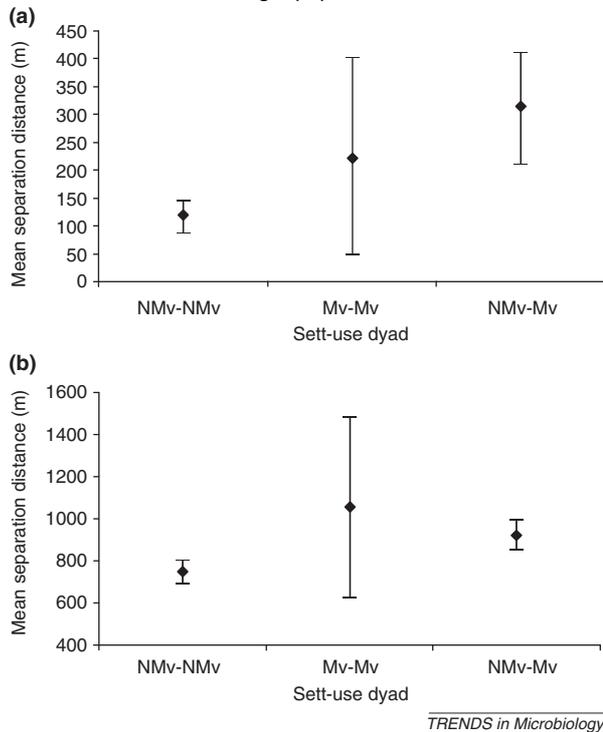
### Box 1. Contact networks in wildlife populations

For group-living carnivores such as badgers, direct interactions between individuals in a population define their social relationships and are important in maintaining the social hierarchy. Individuals that have strong amicable ties might remain within the core group, whereas those individuals receiving high levels of aggression from dominant animals might lead a more itinerant existence or might disperse [60–63]. Members of a group might not all participate in intergroup interactions to the same degree; for example, dominant individuals might be more involved in territorial defence than sub-dominants, or males more than females [64,65]. As a result, direct contact both between members of the same social group and between members of different groups can be highly asymmetrical. Differences in the ‘personalities’ of individuals, known as behavioural syndromes, have become the focus of increased attention from behavioural ecologists in recent years [66,67], but there are few examples of their incorporation into epidemiological research to date. However, these differences between individuals will have implications for disease transmission because certain individuals might exhibit behavioural patterns that put them at a higher risk of becoming infected or passing an infection on to other animals [68].

Few studies to date have aimed to quantify patterns of direct social interactions within wild group-living carnivore populations, primarily because of the elusive nature of many species and the limitations of current remote-surveillance equipment. However, it is possible to investigate the potential for such interactions by using radio tracking to provide simultaneous locations of two or more individuals and then analysing the movement of one individual in relation to the movement of another, known as ‘dynamic interaction’ [69]. In these studies, interactions are defined as occurring when two individuals are found within a specific distance of each other (defined by the resolution of the radio-tracking regime).

Using this type of approach for badgers, Böhm *et al.* [37] showed that intragroup separation distances were significantly shorter than intergroup separation distances and that interactions between groups are rare. Within groups, individuals interact with each other more often than expected based on neutral movement models, and interaction patterns vary significantly with season and sett-use pattern. Almost 90% of close intragroup interactions were associated with the main sett. Badger dyads (pairs of animals that are not necessarily associated with one another socially or sexually) displayed different patterns of contact behaviour according to their patterns of sett use. Dyads of non-mover animals (i.e. animals that predominantly use the main sett) and dyads of non-movers and movers (i.e. animals that tend to use outlying setts) interact significantly more often at the main sett than mover-only dyads (Figure 1). These observations highlight the fact that badger social groups comprise different subgroups, which show different patterns of contact behaviour. These asymmetries will affect the way in which diseases are transmitted through a social network, both within and between species. Mean field models of disease spread that assume consistent behaviour across specific age or sex categories may, therefore, give misleading results when applied locally. Further quantification of these networks, which has now been made possible by the availability of proximity data loggers, is essential for understanding the

persistence and spread of bTB locally within badger populations and among badgers and cattle, and potentially could be used to identify high-risk individuals within badger populations and cattle herds.



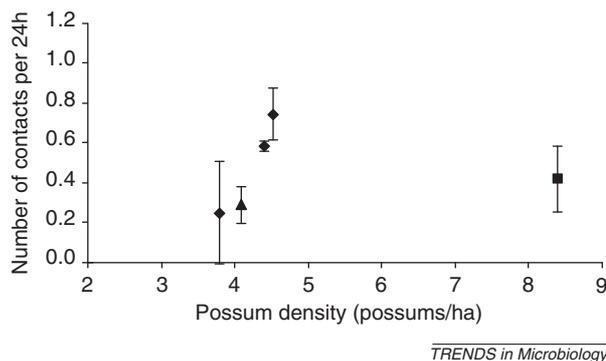
**Figure 1.** Mean separation distances  $\pm$  standard error of the mean for (a) intragroup and (b) intergroup dyads. Mv, mover animals; NMv, non-mover animals. Reproduced, with permission, from Ref. [37].

### Box 2. Contact-rate–density relationships among hosts

The reduction of wildlife populations to control disease in livestock is based on the principle of transmission by mass action. Because the transmission rate is assumed to be positively and linearly related to a product of the density of infectious and susceptible hosts [53,54], the premise is that a reduction in the density of either class of hosts will lead to a reduction in transmission opportunities for the infection. This assumption has underpinned the majority of livestock–wildlife disease-control strategies in the past, including those for the control of bTB in the UK. However, for some infections that rely on a specific type of contact (such as sexually transmitted diseases), the contact-rate–density relationship is non-linear and reaches an asymptote at relatively low densities. This same pattern might be replicated for infections that can be transmitted by other forms of contact but for which the opportunities for transmission rely on specific behavioural patterns to bring animals together.

In contrast to badgers, which are group-living animals, the principal host for bTB in New Zealand, the brush-tailed possum, is a solitary animal for most of the year, with mature individuals usually only coming together to mate. Mating activities, therefore, provide the greatest opportunity for bTB transmission among possums. Ji and co-workers, using recently developed proximity data loggers across three distinct populations of possums, were able to quantify this type of non-linear contact-rate–density relationship for the first time [34] (Figure 1).

For bTB in Britain, deriving such relationships for badgers would represent considerable progress for underpinning the development of control strategies. However, it is important to recognize that contact patterns within badger populations are just part of the system. To move to the next level in terms of both epidemiological understanding and applied disease control, we need to use this technology to quantify such contact-rate–density relationships among the complete host community.



**Figure 1.** The relationship between the mean monthly male–female-contact rates during the peak breeding months at Coatesville (diamonds; 1999, 2000 and 2001), Huapai (triangles; 1999) and Mangatiwhiri (squares; 1999), North Island, New Zealand. Data from Ref. [34].

### **Box 3. Methods used to derive the risk maps**

#### **Livestock distribution**

Cattle risk classes were based on cattle densities at the 10-km square level; the densities were derived from livestock numbers at the local authority (LA) level obtained from the 2003 Agricultural Censuses for England, Scotland and Wales ([http://www.defra.gov.uk/esg/work\\_htm/publications/cs/farmstats\\_web/Publications/complete\\_pubs.htm](http://www.defra.gov.uk/esg/work_htm/publications/cs/farmstats_web/Publications/complete_pubs.htm)); <http://www.scotland.gov.uk/library5/agri/sacs03-00.asp>; <http://www.wales.gov.uk/keypubstatisticsforwales/content/publication/agriculture/2004/was2003/was2003-ch2/was2003-ch2.htm>). Data for England were used at the LA level, which was the most appropriate scale for this analysis. Census data for Scotland were available at the LA level, although the LA area is considerably larger than in England. Census data for Wales were available at a regional level only, again resulting in lower-resolution data. Using GIS, each 10-km grid square in Britain was assigned to its corresponding LA or region, and the mean livestock number per square was calculated by dividing the total number of livestock within the LA or region by the number of 10-km squares assigned to it. This was converted to livestock densities per km<sup>2</sup> at the 10-km square resolution. In some cases in the English census data, no livestock numbers were published at the LA level. Those LAs using only county-level livestock numbers were repopulated, having first adjusted these data by subtracting known livestock numbers for individual LAs from the county total. 10-km square density values were grouped into six groups (0–5) based on the number of standard deviations each was away from the mean, and risk scores were assigned to each group in order of ascending density.

#### **Badger distribution**

Badger risk classes at the 10-km square level were based on average probabilities of badger main-sett presence per km<sup>2</sup> using the predictive species-habitat model developed by Newton-Cross *et al.* [49], which represents a notable advance over previous badger-habitat models in accuracy and spatial resolution. The most important habitat types for predicting main-sett presence and absence were matched with 1-km square habitat subclass data from the CEH Land Cover Map 2000, and the probability of badger presence for each 1-km square was calculated. The average probability across all 100 1-km squares in a given 10-km square of main-sett presence (per 1-km square) for each 10-km square in Britain was obtained. These average probabilities were grouped into six groups (0–5) based on the number of standard deviations each was away from the mean, and risk scores were assigned to each group in order of ascending probability.

#### **Deer distribution**

There are no reliable spatial data or models of deer abundance for most of Britain [70], but species richness of deer has been shown to correlate with deer abundance at a regional scale (<http://www.woodlandforlife.net/wfl-woodbank/DisplayArticle.asp?ID=2333>) and more species-rich deer communities can be considered as representing a higher risk for acting as a host for disease. Deer risk classes were, therefore, based on the number of deer species occurring in each 10-km square [52]. Owing to their infrequent occurrence, squares with five or more deer species were grouped together in the highest relative risk category, giving six risk classes overall (0–5) for deer.

#### **Overall risk scores**

Based on the assumption that infection risk increases as a function of the complexity of the wildlife host community, a similar multiplicative relationship between the relative risk scores of each of our potential bTB host groups (cattle, badgers and deer) was used to give an overall risk score for each 10-km square, which was then plotted to produce the risk maps in Figure 1 (in main text).