Biological hurdles to the control of TB in cattle: A test of two hypotheses concerning wildlife to explain the failure of control

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ABSTRACT

Since the 1970s the control of bovine tuberculosis (bTB) in cattle, predominantly in the SW of England has proved continually recalcitrant; it is currently increasing at an annual rate of 18%. This deterioration has occurred despite a succession of government schemes involving killing badgers, Meles meles, with the intention of reducing transmission of bTB to cattle. Of various hypotheses proposed to explain this failure of control, some concern agricultural practice, but two concern wildlife. The latter are, first, that wild mammalian species other than badgers are important in the transmission of bTB, and second, that a perturbation effect amongst those badgers surviving a cull countermands the hoped-for reduction of bTB transmission to cattle or even increases it. We review our own studies of these two hypotheses in the context of other findings. We conclude that the other species hypothesis does not provide a general explanation for the failure of bTB control. We also conclude that the perturbation hypothesis is supported by the data and does provide one plausible mechanism to explain why culling badgers has not generally achieved control of bTB in cattle. We have reviewed the relevance of perturbation with respect to three key questions:

(a) is there evidence of a perturbation effect on badger behavioural ecology?
(b) is there evidence of a perturbation effect on prevalence of bTB in badgers?
(c) are any observed effects of a magnitude relevant to bTB control policy?

The results of the Randomised Badger Culling Trial (RBCT) and our own studies indicate that to have any prospect of contributing significantly to controlling bTB in cattle, a badger cull would have to be undertaken over a very large area. Considering the likely very important role of cattle-to-cattle transmission, and the opportunities for solutions in terms of farm management and surveillance, it would be inappropriate (and probably impractical) to undertake such a cull now.
1. Introduction

Mycobacterium bovis, the causative agent of bovine tuberculosis (bTB) infects a wide range of mammals. In the UK it was formerly an important human disease but it is now primarily of veterinary concern. In cattle, routine test-and-slaughter regimes drove down bTB prevalence, until the 1970s when, nationally, it was reduced to \(0.05\%\), though a higher incidence persisted in South West England. Unfortunately, and despite continued cattle-based control measures, bTB incidence has risen over the last 30 years. The current rate of increase is c. 18\% pa. (Fig. 1a). bTB 'hot-spots' have also re-emerged outside the South West, and within these Woodroffe et al., 2005 found that TB-affected herds were closer to other affected herds than would be expected if the distribution of infection within the population was random. Cattle movements, particularly those from areas where bTB is reported, are the best predictor of disease occurrence (Gilbert et al., 2005).

Internationally, bTB control has proved difficult to achieve where there is a persistent reservoir of infection in wildlife (Morris et al., 1994). In the UK, badgers have been culled since 1971, when a tuberculous dead badger was found on an infected farm (Table 1). Interpreting subsequent trends in incidence are complicated by multiple factors; for example, changing specificity of tests (Clifton-Hadley et al., 1995b), changes to the cattle farming industry (Table 2) including, pollution control regulations (The Water Resources Act) in 1991 resulting in a drift from slurry-based restrained housing systems towards loose housing, while levels of aflotoxins in feed, known for their immunosuppressive qualities, have increased (Farm Animal Welfare Council, 1997). These and many other factors may have bearing on the bTB figures, which also vary with aspects of habitat management (Mathews et al., 2006b). Furthermore, the increases in bTB in cattle have been associated with increases in both badger numbers (Krebs, 1997; Wilson et al., 1997) and the proportion of badgers removed in culling operations found to be tuberculous (Fig. 1b). Recent analyses have also demonstrated spatial associations locally between M. bovis infection in cattle and badgers (Woodroffe et al., 2005).

Of 2692 adult badgers killed from 1998 onwards in an unbiased sample from within ten 100 sq. km hotspots of bTB prevalence in cattle, 12\% were culture positive (14.4\% of males and 10.0\% of females (Woodroffe et al., 2005)). The question arises as to how much worse (or better), things might have been in the absence of the badger control programmes. If success is defined as slowing down and preventing the geographic spread of bTB to areas currently free of the disease, and achieving a sustained reduction in disease incidence in cattle in high incidence areas. (DEFRA, 2005, “Government strategic framework for the sustainable control of bovine tuberculosis (bTB) in Great Britain”), then it is uncontroversial to conclude that successive badger control policies have failed. In this paper, we review the evidence from our own studies for the two hypotheses formulated to explain this failure in terms of wildlife: the other species hypothesis and the perturbation hypothesis.
As background, M. bovis is a generalist pathogen. The aetiology of infection is primarily respiratory, with the principal disease transmission route being respiratory (O’Riley and Daborn, 1995). Survival of M. bovis outside of a host organism varies depending on environmental conditions (King et al., 1999) and environmental Mycobacterium occur on a large proportion of cattle farms in endemic bTB regions in the UK (Courtenay et al., in press-a, in press-b).

![Graph showing percentage of cattle herds infected with bovine tuberculosis between 1962 and 2003 and numbers of captured badgers caught and percentage prevalence of bovine tuberculosis diagnosed post-mortem from 1982 to 1997.](image_url)

Fig. 1 – (a) Percentage of cattle herds in the southwest and remainder of Great Britain infected with bovine tuberculosis between 1962 and 2003, presented on the Defra web-site (www.defra.gov.uk). Data available up to 1998 include both confirmed and unconfirmed reactors, whilst data available from after 1998 include only confirmed reactors and are thus a more conservative estimate. Data are excluded from 2001 due to disruption to cattle testing as a result of the foot and mouth disease outbreak. (b) Numbers of captured badgers recorded from badger removal operations throughout the UK (left axis) and percentage prevalence of bovine tuberculosis diagnosed post-mortem (right axis) from 1982 to 1997 (illustrating general trends, but complicated by spanning periods when different protocols were used) (source: www.defra.gov.uk).

<table>
<thead>
<tr>
<th>Date</th>
<th>Action</th>
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<tr>
<td>1971</td>
<td>bTB +ve badger found on reactor farm</td>
</tr>
<tr>
<td>1973</td>
<td>Farmers carry out culling</td>
</tr>
<tr>
<td>1975</td>
<td>Large scale gassing of badger setts</td>
</tr>
<tr>
<td>1980</td>
<td>Zuckerman Report</td>
</tr>
<tr>
<td>1982</td>
<td>Gassing ceases</td>
</tr>
<tr>
<td>1982</td>
<td>Trapping starts – clean-ring strategy</td>
</tr>
<tr>
<td>1986</td>
<td>Dunnet Report – &quot;interim strategy&quot;</td>
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<tr>
<td>1994</td>
<td>Experimental live-test strategy</td>
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<tr>
<td>1997</td>
<td>Krebs’ Report</td>
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<tr>
<td>1998</td>
<td>Randomised Badger Culling Trial (RBCT)</td>
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<tr>
<td>2003</td>
<td>Cessation of reactive strategy in RBCT</td>
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Table 1 – Chronology of control measures against badgers in UK

<table>
<thead>
<tr>
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<tbody>
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<td>1970</td>
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<tr>
<td>1970</td>
<td>3750</td>
</tr>
<tr>
<td>1995</td>
<td>5395</td>
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Table 2 – Changing characteristics of UK dairy farming during the period of increasing incidence of bTB in cattle


As background, M. bovis is a generalist pathogen. The aetiology of infection is primarily respiratory, with the principal disease transmission route being respiratory (O’Riley and Daborn, 1995). Survival of M. bovis outside of a host organism varies depending on environmental conditions (King et al., 1999) and environmental Mycobacterium occur on a large proportion of cattle farms in endemic bTB regions in the UK (Courtenay et al., in press-a, in press-b).
The ability of M. bovis to colonise a wide range of host species is well-established (Francis, 1958). Two groups of animals susceptible in the laboratory – rodents and lagomorphs – are particularly numerous and widespread on farmland. However, reviews of bTB control in Britain consistently highlighted the lack of adequate information about the role of wildlife other than badgers in the epidemiology of bTB (Krebs et al., 1997; MAFF, 1987; House of Commons Agriculture Committee, 2003). It was even unclear which species are infected in the wild. bTB had been identified post-mortem in ferrets (Mustela putorius furo), moles (Talpa europaea), rats (Rattus norvegicus), foxes (Vulpes vulpes), mink (Mustela vison) and deer (roe; Capreolus capreolus: red; Cervus elaphus: fallow; Dama dama: and sika Cervus nippon) (MAFF, 1987). Of these only ferrets and deer are thought to be potentially infectious (i.e. excreting viable organisms) (Krebs et al., 1997; Delahay et al., 2002), although bTB had also been isolated from a voles, species unknown (Delahay et al., 2002). In the USA bTB appears to be transmitted from deer to livestock (Schmitt et al., 2002; Wilkins et al., 2003); and in Spain, where deer and livestock from the same location share the same spoligotype of bTB (Arana et al., 2004), and where genetic heterozygosity of wild boar is a predictor of their susceptibility to bTB (Acevedo-Whitehouse et al., 2005). M. bovis had not been reported in any other wild British mammal (MAFF, 1987). However sample sizes have generally been low.

Against this background, we set out to obtain robust estimates of the prevalence of individuals infectious for M. bovis, to investigate epidemiology and molecular type of bTB in wildlife, and to quantify the risk to cattle from bTB infection in wildlife. Deer were excluded from our survey, but were the subject of a companion survey by our colleagues at CSL (Delahay et al., in press). We focused on determining the prevalence of infectious animals since this is a key parameter in epidemiological models of disease transmission and control. In addition, the use of live-sampling enabled us to obtain large sample sizes within farms – something that would not be possible due to ethical and ecological concerns – with lethal sampling.

Complete details of the survey methodology are provided elsewhere (Mathews et al., 2006a). Briefly, our surveys were conducted on 12 dairy farms, arranged as four ‘triplets’ in the following geographical areas: Staffordshire/Derbyshire; North Somerset; Carmarthenshire; and Gwent. Each ‘triplet’ comprised two ‘case farms’ (>1 breakdown confirmed by culture of M. bovis from tissues of culled cattle since 1997 and >2 incidents of positive reactors to the tuberculin skin test since 1997) and one randomly selected control farm (no confirmed breakdowns and also no reactors since 1994).

On the first seven farms (5 case, 2 control) we aimed to “live-sample” a representative sample of all terrestrial species present on study farms. For the remaining farms we focused on just small mammals (<30 g), rabbits, squirrels, rats, present on the farm, together with all domestic or feral cats and dogs. Badgers were trapped throughout the study on 4 case and 2 control farms, except during the ‘closed’ season (January–May inclusive). One additional animal was caught during a short trapping period on a further case farm.

Animals were sampled under gaseous anaesthesia (Mathews et al., 2002). Specimens of tracheal aspirate, faeces and urine were collected from each individual, and transported and refrigerated, within 24 h for microbiological culture.

Samples were decontaminated using the N-acetyl-l-cysteine–NaOH digestion–decontamination procedure (Kent and Kubica, 1985; Collins et al., 1997). Different strains of M. bovis are known to vary in their preferences for different media, with some strains failing to grow at all on particular media types. We therefore used agar-based (modified Middlebrook 7H11), egg based (acidified Jowenstein Jensen with pyruvate Lp), and liquid BACTEC MGIT 960 medium for each sample. All presumptive positives were confirmed by PCR. These were: PCR for IS1081, a multi-copy element generally present in six copies in members of the M. tuberculosis (MTB) complex (Dziadek et al., 2001). Additional PCRs were used to detect and distinguish between M. microti and classical M. bovis (Gordon et al., 1999). PCR-based typing (Spacer-OLIGOnucleotide TYPING – ‘spoligotyping’) was conducted to determine strain-types as previously described (Arana et al., 1996). In addition, we employed PCR directly on our samples as a second, independent, diagnostic test. This test was based on the HSP65 gene which is specific for M. tuberculosis complex organisms (Sechi et al., 1999; Telenti et al., 1993; Sreevatsan et al., 2000). Presumptive positives were speciated using sequencing. Unlike culture, PCR identifies any excreted bacilli, not just live organisms. A positive result by PCR therefore does not constitute absolute proof that the individual was infectious.

Live culture revealed only one positive bank vole, Clethrionomys glareolus (Table 3). This isolate was obtained from tracheal aspirate, which implies that the animal had developed systemic disease. The strain type was the same as that identified on badgers and cattle on the same holding (strain SB 0673). Further PCR work, which is ongoing, has confirmed another positive bank vole, 4 positive wood mice and one rat (but this test cannot distinguish live organisms, making it impossible to determine whether these animals were infectious). We built deterministic models using life history parameters of the host and disease prevalence to investigate the likelihood of the disease persisting in each of the host species, at the prevalences seen in the field. Initially we assumed that no between-species transmission was present. Using the prevalences seen in the field, and assuming that the system is at equilibrium, we computed the basic reproductive number $R_0$ for each of the species, using the fact that for this model, prevalence = $1 - (1/R_0)$. The analyses showed that even when the maximum likely prevalence was assumed (based on the upper 95% confidence limit), the $R_0$ (the basic reproductive rate of the disease) ranged from just 1.003 in wood mice to 1.05 in rats (The lower confidence intervals for prevalence always gave $R_0$ values that were <1.0) (Mathews et al., 2006a). It is therefore unlikely that the disease would persist within single-host systems in the...
Culling is often used in attempts to manage wildlife disease. – are significant reservoirs of bTB can be rejected.

Farmland, we conclude, following modelling, that the hypothesis of complicated transmission pathways for bTB on badgers can share the same strain type (SB0673), raising the possibility that susceptible individuals become infected.

Those we have observed in the field.

To materially affect the R₀, the prevalences would need to be have been underestimated very substantially. If, instead of single-host models, we assumed multiple-host systems with the previously estimated within-species transmission rate, then the additional between-species transmission would lead to prevalences higher than those we observed in the field. Alternatively, in order to achieve the prevalences seen in reality, the within-species transmission rate would have to be even lower than that estimated above. Multi-species transmission of bTB within farmland wildlife communities therefore appears unlikely. Even spill-over events from badgers and cattle must be very rare in order to achieve prevalences as low as those we have observed in the field.

Although we have confirmed that bank voles, cattle and badgers can share the same strain type (SB0673), raising the possibility of complicated transmission pathways for bTB on farmland, we conclude, following modelling, that the hypothesis that common wildlife – small mammals and lagomorphs – are significant reservoirs of bTB can be rejected.

3. The perturbation hypothesis

Culling is often used in attempts to manage wildlife disease. The perturbation hypothesis postulates that killing individuals may affect the survivors in ways (behavioural, physiological, immunological) that cause a disproportionate, and perhaps counter-productive, effect. This idea, first published in the context of badgers and bTB by Overend (1980), has potentially wide relevance in wildlife management (e.g. Tuyt tens and Macdonald, 2000). An early model by Swinton et al. (1997) demonstrated that perturbation had the potential to be a counter-productive factor in control of bTB in badgers. This could occur when the complete or partial emptying of territories might change spatial organisation, alter frequency and tenor of social interactions and change demography and reproductive biology. Each of these factors might affect the probability of transmission (and thus the reproductive rate of the disease) within badgers and between badgers and cattle. In addition, the stress associated with perturbation may cause immuno-suppression, both increasing the rate at which bacilli are shed (because disease is further progressed), and increasing the risk that susceptible individuals become infected.

Here, we consider three questions: (a) is there evidence of a perturbation effect on badger behavioural ecology, (b) is there evidence of a perturbation effect on prevalence of bTB in badgers and (c) are any observed effects of a magnitude relevant to bTB control policy?

These questions lay behind a suite of studies undertaken in the south west of England and begun in the mid- to late-1990s. Some, such as the two we report below, focused on the behavioural ecology of badgers at the individual level in an attempt to describe perturbation effects at the scale of individuals and social groups. Other studies, notably the Randomised Badger Culling Trial (RBCT) proposed by Krebs et al. (1997), adopted a large-scale experimental approach, monitoring the incidence of bTB in badgers and cattle in large areas exposed to different control regimes. Results of these studies are simultaneously becoming available, combining to revolutionise knowledge about social perturbation and its impact on wildlife disease epidemiology. Of the large-scale experimental studies, the studies of Woodroffe et al. (2005, 2006) and Donnelly et al. (2005) add to Donnelly et al. (2003) in demonstrating that badger culling has not been associated with a clear cut diminution of bTB in cattle. On the contrary, whereas at the centre of 100 sq. km plots from which badgers have been pro-actively removed, there may be a lowering (by c. 15%) of bTB in cattle, up to at least 2 km from the borders of these areas infection in cattle increased (by c. 29%). Similar results were found in comparable areas where clusters of badgers were removed reactively, following nearby outbreaks of bTB in cattle (Donnelly et al., 2003). Our own studies, which we now review, complement this broad-scale approach by providing data on individual behaviour. Taken together, all these findings make it clear that pertur-
bation effects are indeed relevant to the control of bTB in badgers (Carter et al., submitted for publication).

3.1. Undisturbed badgers

First, what is known about undisturbed badgers, their sociality and how this might affect the manner in which bTB behaves amongst them? Since pioneering work by Kruuk (1978a,b, 1989), badgers are amongst the most thoroughly studied mammals in lowland Britain, most especially through two long-term studies in Wytham Woods, Oxfordshire (51°46'N, 1°20'W) and Woodchester Park, Gloucestershire (51°42'N 2°15'W) (Delahay et al., 2000; Macdonald and Newman, 2002). In lowland Britain undisturbed badgers live territorially, in stable mixed-sex groups of up to 30 individuals, sharing communal dens (setts). Individuals within a social group interact closely and conflict leading to bite wounds is frequent (Macdonald et al., 2004; Delahay et al., 2006). Although long-term dispersal is infrequent (Rogers et al., 1998; Macdonald et al., submitted for publication), short-term excursions between social groups are common (Woodroffe et al., 1993) and involves mating (Macdonald et al., submitted for publication; Evans et al., 1989; Carpenter et al., 2005). In undisturbed populations the territories can be neatly tessellated and ringed by shared latrines (Kruuk, 1978).

There has been only one detailed study of M. bovis epizootiology in undisturbed badgers, which followed the progress of infection in the Woodchester Park population between 1982 and 1996 (previous culling of badgers there ceased in 1978) (Delahay et al., 2000). This showed that bTB does not spread rapidly at high incidence through badger populations, but rather is distributed patchily amongst a minority of individuals. Rogers et al. (1998) reported a correlation between rates of inter-group movement at Woodchester and the incidence of new infections. While spatial clusters of infection existed there was no strong synchrony between neighbouring groups, with transmission rates between them being low. This pattern is compatible with the finding by Woodroffe et al. (2006) that amongst badgers killed in the proactive RBCT, infected badgers were closer to other infected badgers than would be expected if the distribution of infection within the population was random. Within infected groups, bTB may persist due to the continual input of susceptible individuals through births (fecundity is unaffected by bTB infection until chronic (Wilkinson et al., 2000; Clifton-Hadley et al., 1993)) and acquired immunity remaining low (Gallagher and Clifton-Hadley, 2000).

3.2. Two field studies of perturbation

We, together with our collaborators at the Central Science Laboratory have undertaken two large-scale field studies of badger social perturbation. The first, at North Nibley, Gloucestershire compared the biology of the badgers, and prevalence of bTB, before and after attempted control by culling. The second, the Triplet E Experiment (TEE), made similar comparisons before and after attempted control, but also included a control area where no culling was undertaken. In both experiments, observations made in the two long-term studies, at Woodchester Park and Wytham Woods, provided comparative controls of undisturbed populations in lowland environments. The primary results of our findings at North Nibley are reported in Swinton et al. (1997), Tuyttens et al. (1999), Tuyttens et al. (2000a,b,c) and Riordan et al. (submitted for publication-a), whereas the primary results from Triplet E are published as Riordan et al. (submitted for publication-a, submitted for publication-b). Here we review these findings.

3.2.1. The study sites

3.2.1.1. The North Nibley case study (1995–2000). In January 1995, a herd breakdown at North Nibley (51°39’N, 2°22’W) was attributed to badgers by UK government officials. At that time, policy was randomly allocating badger control to two protocols, the Live Test strategy and the Interim strategy. The study area measured 17 km², within which there had been 12 badger-culling interventions in the preceding 20 years (Fig. 2). This level of repeated interventions is not exceptional in SW England and raises the point that, depending on the duration of any perturbation effects, badgers throughout much of the region may be persistently perturbed.

Between January and September 1995 our team mapped 42 setts, marked 62 individual badgers and estimated the population at 150, of which 14 were radio-tracked. Bait marking allowed us to plot 558 latrine sites, in the vicinity of the breakdown farm and map social group boundaries. In September, undertaking a Badger Removal Operation (BRO) using the Live Test strategy, government officials tested badgers from 14 social groups for bTB using an ELISA live-test. Six groups (associated with eight setts) were identified as infected (including one from which two badgers had been culled five years earlier), and 27 badgers were killed from these, together with an additional badger that was shot by mistake from a non-infected group. In total, badgers were trapped in an area of 6.5 km². Typically, setts were trapped until no signs of badger activity were apparent, the numbers of badgers killed per sett varied between 1 and 7.

In June 1996, a further 2 badgers were trapped and killed in an Interim Strategy BRO. The Interim Strategy (IS) involved attempting to trap all badgers on ‘reactor land’, that is the farm on which bTB transmission was thought to have occurred. In this case the IS involved an area of only 0.2 km².

At North Nibley, comparing estimates for June in 1995 and 1996 suggests that the population of the 17 km² fell from 145 to 118, a fall of 27 animals (in line with the 29 culled). We monitored the badgers until November 2000.

3.2.1.2. The Triplet E experiment (2000–2004). In the RBCT, a proactive and a reactive culling strategy were tested against a control (i.e. survey-only) in ten triplets (c. 100 sq km each). In one of the Triplets, E, we established a study area (~40 km²) within the reactive treatment and a comparative control (~20 km²) in the survey-only area (Riordan et al., submitted for publication-b, submitted for publication-c). Although this work started in late 2000, it was almost immediately interrupted due to the UK foot and mouth disease (FMD) outbreak in 2001. Fieldwork recommenced in October 2001, and four BROs were observed before the fieldwork ended in December 2003 (Fig. 3). Seventy seven badgers were killed, amounting to about 34–43% of those resident in the targeted setts.

As with our study in North Nibley, badger social groups within the treatment population were categorised as
either “Removed”, “Neighbouring” or “Other”, whilst groups within the survey-only populations were labelled “Control”.

Six hundred and sixty-three captures were made (overall, 29% of individuals were caught more than once, 28.3% and 30.1% for males and females, respectively). Prior to the first culls, the estimated densities of the treatment and control populations were c. 5 badgers km\(^{-2}\). The BROs in the winter of 2002–2003 removed 44 badgers, coinciding with a seasonal decline due to losses over winter in the survey-only zone. The second two culls, in August 2003, removed a further 33 animals.

3.3. Question (1): Is there evidence of a perturbation effect on badger behavioural ecology?

3.3.1. (a) Demography

Fig. 4 reveals that the Nibley population took five years to recover. Furthermore, the growth rates and final weights of cubs reared at North Nibley were substantially higher than those of their counterparts at Woodchester and Wytham every year until 2000 (Fig. 5).

Comparison with the population trends at Woodchester Park and Wytham Woods suggests two processes appear to be at work at North Nibley (a) a local recovery from culling and (b) a regional increase (perhaps associated with ameliorating climate, Macdonald and Newman (2002)).

Demographic effects of culling with the TEE were complicated by differences in the seasonal timings of culls within the treatment study area. Badger removal operation (BRO) 2 occurred in autumn 2002, BRO 4 took place in winter 2003 and BROs 7 and 9 occurred in summer 2003, when badgers move more and may be more motivated to disperse. In the treatment population, badger movement was greatest in...
summer, although this was not the case in the control, where individual movement was greatest in autumn (Riordan et al., submitted for publication-c). However, group sizes in the control population increased in the post-culling period, whilst those in the treatment population declined, suggesting an overall impact of culling across the treatment population, although the sizes of social groups of each type within the treatment population (Removed, Neighbouring and Other) did not change as a result of culling.

At North Nibley, annual productivity, i.e. cubs produced per female showing signs of reproduction upon capture, varied erratically in those groups not directly subjected to culling, whereas it fell to zero in 1996 in the six groups from which badgers had been removed in 1995. Over the years 1997–1999 productivity increased markedly, potentially reflecting an Allee effect, with population growth rate positively related to density (Courchamp et al., 1999). The net effect, across the 17 sq. km study area, was no difference in overall productivity between removed and non-removed groups over five years. Culling interventions at this scale are thus likely to need to be repeated frequently if they are to suppress populations.

Changes in the productivity of social groups following culling were significantly different in the treatment and control populations of the TEE, with a decline in Removed groups and an increase in Neighbouring groups. However, in
3.3.2. (b) Dispersion and spatial organisation

At North Nibley in 1995, culling largely targeted areas of highest badger density (in effect, the largest social groups). By 1999, the distribution of badgers in the study area was radically different from that at the outset (Fig. 6). Thus while the population density recovered as a whole, the badgers built up in a different place. The increased membership of groups

Fig. 6 – Interpolated visualization of badger density across the North Nibley study area between 1995 and 1999. Social groups removed in 1995 are shown as black crosses, with the symbol size indicating the number of animals culled. Social groups not culled in 1995 are shown as white dots.
in the non-culled parts of the study area may have arisen partly due to the reduced reproduction amongst survivors and colonists of culled groups, and the tendency of animals to emigrate from smaller groups. Whatever the mechanism, culling was followed by a redistribution of the badger population at Nibley.

In both the North Nibley study and the TEE, the spatial arrangement of badgers was determined by bait-marking (Kruuk, 1978). In both cases, at the outset the mosaic of ranges was more chaotic than is typical of undisturbed populations (e.g. Fig. 7). In both studies the general extent of overlaps between groups increased following culls (e.g. Fig. 8a), as did the numbers of ranges with which each group overlapped (e.g. Fig. 8b). At Nibley these measures of overlap remained elevated for the four succeeding years, and no new territories were established as the population recovered (extra badgers were accommodated by increasing group sizes). At E1 the numbers of overlaps increased for removed groups and their Neighbours, but it fell for Other groups. It also fell in the survey only area, E2. Radio-tracking revealed that the number of other non-group individuals overlapped by the movements of radio-collared badgers increased about fourfold following the winter cull in 2002–2003 for members of Neighbouring and Other groups. In contrast, in E2 there was no such change. In summary, there is evidence of a perturbation effect in altered spatial organisation and individual movements.

In the TEE, as a measure of social stress directly linked to disease transmission we recorded the levels of aggression through the proportion of badgers receiving fresh bite wounds. The overall rate was 22.6% for males, which seems high considering that in Wytham Woods the comparable figure was 24.9% in a population at 8–9-times the density, and within which bite-wounding increased with population density (Macdonald et al., 2004). This might be related to the history of culling in both the TEE study areas. The proportion of badgers with fresh bite wounds changed significantly following culling, with significant increases in Neighbouring and Removed social groups following the winter 2002/2003 BRO in the treatment population. However, contrary to prediction, the largest increase in bite wounding was in E2 in September/October 2003 (see below).

Rates of bite wounding observed in the North Nibley populations tended to be lower than that observed at Wytham Woods and Woodchester Park, though not significantly so (Delahay et al., in press). In contrast to the TEE findings, bite wounding in the North Nibley population decreased immediately following culling in 1995 and then increased steadily, reaching a peak in 1998. In contrast to the populations in Wytham Woods, Woodchester Park and the TEE, wounding in North Nibley was more likely in females. This may be related to the early recolonisation of setts by females (see below) and the demographic outcomes following culling, where the population became female biased.

### 3.3.3. (c) Dispersal

At Nibley, we believe no badgers survived the BRO in four of the six removal groups (in one group a female cub survived, and in another a male cub and an adult male survived). In

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**Fig. 7 – 1999 Bait marking ranges of badger social groups in North Nibley, expressed as 95% minimum convex polygons (MCP). Bold MCPs show social groups containing badgers infected with bTB in North Nibley, with the numbers of infected animals within groups denoted by variable size dot markers indicating main sett locations.**
In contrast, in the TEE treatment area in no case was a group entirely emptied of occupants and with only c. 40% of badgers culled from targeted groups, sufficient animals remained after the November 2002 and January 2003 culls for all of the Removed groups to have produced young in 2003. In the emptied home ranges at Nibley the first colonists were all female, in all cases yearlings from adjacent social groups. The female cub that had survived alone moved to a non-adjacent group (and several other groups subsequently), while three females of a neighbouring group started to move into its vacated range, and two eventually settled there (the third remaining in its original group). In the first and second years after the BRO, one and three adult females, respectively, were captured in the group where a male cub and adult had survived the culling operation. The origins of all four females were unknown. The male cub was never trapped again, but the adult male stayed in its natal group until the end of 1997.

Even in undisturbed setts within the Nibley study area, badgers not only dispersed from their natal group, but also made excursions, defined as capture events where a badger is trapped at a different group to its previous capture. Such excursions comprised 10.14% of 759 captures at North Nibley, much fewer than comparable figures of 44% and 65% reported for Woodchester and Wytham, respectively (Macdonald et al., submitted for publication; Rogers et al., 1998). Such inter-group movements were even more uncommon in the TEE: of 663 trapping events in the treatment and control populations, only 12 instances of badgers moving between social groups were detected (11 individuals). Of these, nine (75%) occurred in the treatment population following the culls in the winter of 2002–2003, and only one inter-group movement was detected during six trapping events in the control population. Combined inter-group movement events from trapping and radio-tracking, yielded a total of 14 episodes, of which 12 were post-culling in the treatment population; five of these being moves from Neighbouring social groups and four being survivors from Removed groups. Badgers were more likely to move to a Removed group, with all of the 10 moves from Neighbouring or Other groups being to Removed groups. Thus, following culling, badgers were more likely to move from Removed and Neighbouring groups than from Other and Control groups (badgers were also more likely to move from large groups).

Thus, culling was associated with an increased rate of inter-group movements (it may also have affected some other behaviour patterns, such as vigilance (Tuyttens et al., 2001)).
However, even after culling, the rate of inter-group movements in both Nibley and Triplet E was lower than in the high density undisturbed populations, perhaps because a history of culling maintained both of the former substantially below carrying capacity.

In summary, at the levels of individual behaviour, and the local arrangements of badger populations, the studies at North Nibley and Triplet E demonstrate that there is a perturbation effect of culling on badger behavioural ecology.

3.4. Question (2): Is there evidence of a perturbation effect on prevalence of bTB in badgers?

At both Nibley and Triplet E we monitored the infection status of badgers by bacterial culture of samples of urine, faeces, sputum (by tracheal aspirate) and pus (where available from wounds). In North Nibley samples were collected from 309 individuals, during 868 sampling events. At Triplet E samples were collected from 466 individuals, during 663 sampling events. An enzyme-linked immunosorbent assay (ELISA) test was also used to test badgers for bTB in the North Nibley population between 1995 and 1997.

It is important to mention some characteristics of these tests. An ELISA aims to identify infected individuals, but cannot distinguish animals actively excreting bacilli from those that are not, and individuals with acquired immunity to bTB will also return positive results (Newell et al., 1997). The sensitivity of the ELISA (proportion of infected badgers correctly identified) has been estimated at 41% overall (Clifton-Hadley et al., 1995a), and is particularly poor for animals with subclinical infections, whereas those with evident lesions at post-mortem were correctly identified in 62% of cases. The specificity of the test (percentage of uninfected badgers correctly identified) is 93%.

At Nibley, we tested the badgers before the cull and 14.5% (9/62) were positive to ELISA tests but only 2 (3.2%) were positive on bacterial culture. The ELISA positive animals came from 8 setts, which fell within the ranges of six social groups. When government officials arrived in a subset of the study area (wherein we had recorded 19.4% of badgers positive to ELISA) their sample of 31 badgers revealed 9 ELISA positives, also in six social groups, but only four of these were the same as the groups we had found to be positive. The difference between our findings (19%) and those of the officials (29%) is within the limits of normal variation of the ELISA test.

The removal operation seemed successfully to remove bTB from the badgers at Nibley. Throughout 1996–1999 we tested 258 badgers and none was positive for bTB from bacterial culture of clinical samples (although one badger captured in 1996, and again in 1997, was ELISA positive on both occasions, though remained culture negative). However, despite the lack of evidence of bTB in local badgers, in 1998 two farms at Nibley suffered herd breakdowns, one being the farm which had triggered the 1995 cull. A year later, a further herd breakdown occurred in the north of the study area. During 1997–1999 an average of 38 badgers per year (approximately half the population), had been tested by culture in the vicinity of these farms, and none cultured positive. However, in 2000, clinical samples were taken from 64 badgers of which three (one from one social group, and two from another) were culture positive (prevalence 4.7%) (Fig. 7).

In contrast, as predicted, the prevalence of bTB in the TEE treatment population increased following culling, but contrary to prediction it also did so in the control population. In spring 2002 we identified 53 groups in the treatment population of which three, widely scattered, groups included culture positive individuals. After the cull, 18 groups in the treatment area contained positive individuals and there was a significant increase in prevalence in Neighbouring groups, whereas prevalence decreased in Removed and Other groups (Fig. 9).

Overall, rates of bTB infection in adult badgers remained unchanged after culling, and a cluster of infection arose in the...
west of the study area, where most infected badgers showed signs of kidney or urinary tract infection, with urine samples testing positive for *M. bovis*. One infected individual was identified out of 101 cubs captured in the two years before culling, whilst 8 out of 76 cubs (10.5%) tested culture-positive for bTB after culling. Of these eight infected cubs, four tested positive for *M. bovis* from urine samples, three from sputum and one from a faecal sample. A total sample of 47 cubs failed to reveal bTB among cubs at any time within the control population.

In spring 2002 we identified 27 groups in the control population, of which two contained one culture positive individual each, but his had increased to eight (involving nine individuals) by the time the cull was complete in the treatment population. This result may be due to chance, but it may also have been linked to circumstantial evidence of illegal badger control. Whatever the explanation, reactive badger culling at the scale and efficiency undertaken in the treatment area offered no benefit in terms of prevalence of bTB in surviving badgers, and may have made it worse.

3.5. Question (3): Are perturbation effects of a magnitude relevant to bTB control policy?

Badger population and spatial organisation parameters from the study site in Triplet E were used to enhance a spatially explicit individual-based simulation model (Shirley et al., 2003). This provided a realistic framework to explore reactive badger control as observed in the TEE treatment area, while varying the spatial scale and efficiency with which badgers were removed from targeted social groups (Riordan et al., in preparation). This stochastic model interrogated each badger within the simulated population at six-month time steps, deriving life-history and bTB infection status. The model is process-based, with reproduction, TB transmission, TB-induced mortality, natural mortality and movement probabilities being derived for each simulated badger at each six-month time step.

As an example (Fig. 10), an infected badger population was modelled over 20 years, with an efficient (90%) reactive cull simulated in year 11, targeting five contiguous social groups. Population density declined as a result of the cull, as did overall bTB incidence, but there was a rise in the number of new infections as predicted by the perturbation hypothesis (Fig. 10).

Using the model, Riordan et al. (in preparation) varied the culling area between 1–25 km², explored efficiencies of 60% and 80% (higher than that achieved in our study area), and the consequences of culling in one year or in two successive years. The estimated bTB prevalence following simulated culling was highly sensitive to varying these parameters, and under many scenarios a perturbation effect neutralised or worsened the effect of culling (a similar illustration of the principle of perturbation was achieved with an entirely different modelling approach by Swinton et al. (1997)). For example, whatever the size of the simulated culling (up to 25 km²), bTB was eliminated within the culled zone only when efficiency was set at 80% and culling was repeated for a second year. Of course, the true relationship between culling efficiency and perturbation effects is unknown, but using that simulated in our model, Fig. 11 shows that if efficiency of a single cull was set at 80% bTB prevalence in Removed groups increased with increasing culling area up to over 9 km² and with ever larger culling areas was reduced but not eliminated up to areas of 25 km², whereas the prevalence in Neighbouring groups showed a different trajectory, and increased with culling areas of up to 15 km². Perturbation effects revealed in our field studies, and incorporated into the life histories of individual simulated badgers, appear to have the potential to produce population effects of a magnitude relevant to bTB control policy (e.g. Donnelly et al., 2005).

3.6. Perturbation as a mechanism for failed control

The broader policy framework to which the results reviewed in this section are relevant is a national consultation in 2006 on the policy question of whether badger culling should be used as part of the next phase of controlling bTB in cattle in
Britain. The problem to which culling badgers is a candidate solution is important: farming is important in the economy and in the maintenance of a biodiverse countryside, and we appreciate the seriousness to cattle farmers of bovine TB and the difficulty government faces in managing it. Hence we ask whether the results of our studies reviewed here, and of those now emerging from the RBCT, offer an answer to the policy question. Interim analyses of the RBCT indicate (a) that the Reactive strategy certainly did not reduce bTB in cattle and may have increased it (there was a 25% increase in risk to cattle, Donnelly et al., 2003), (b) the proactive strategy was associated with a 19% reduction in bTB in cattle within the 100 sq. km plots, but this benefit was offset by a 29% increase within the 2 km wide border zone at the periphery; the overall result of badger culling was therefore at best a marginal benefit (Donnelly et al., 2005). Woodroffe et al. (2006) conclude that a plausible explanation for these population level findings is perturbation. At the scale of individuals or social groups our findings, reviewed here, support that conclusion and suggest some mechanisms (and thereby support a growing body of evidence, e.g. Cheeseman et al., 1988; Delahay et al., 2003). Our studies may help interpretation of the RBCT as follows:

3.6.1. Reactive treatment
Where clusters of badgers are killed, as in the RBCT Reactive treatment, perturbation predicts a counter-productive effect. This prediction applies to the Reactive treatment because (like all its English antecedents) by design it involves relatively small culling zones: the counter-productive affect is predicted to arise partly because the smaller a culling zone the relatively longer will be the perimeter along which perturbation will be provoked, and partly because any inefficiency in culling is predicted to cause perturbation amongst the survivors within the removal area. This prediction appeared to be fulfilled when, in November 2003, an interim analysis revealed that the rate of herd breakdowns in the RBCT increased by 27% in comparison to the survey-only areas (Donnelly et al., 2003). However, the effect was observed rapidly – in one case less than one month after the badgers were removed. This raises the question of how quickly perturbation can occur, and at the level of individual badger behaviour our results show it can be immediate (cows, having become infected become positive to tuberculin tests in about three weeks). However, perturbation is not the sole factor causing control to fail, and badgers are not the sole cause of bTB transmission.

The RBCT reactive areas had, like North Nibley, a long history of attempted badger control, and thus it is to be expected that they were all characterised at the outset by at least somewhat perturbed badger populations. Furthermore, the effectiveness of the culling can vary greatly, as illustrated by the different outcomes of BROS at North Nibley and the TEE. In the TEE treatment population infectious badgers survived in both the removed sets and their neighbours. If this was general, two questions arise: is it likely that removing a third to a half of infectious individuals will (a) reduce the reproductive rate of the disease helpfully within badgers and (b) produce a perturbation effect. The answers are, respectively, no and yes. Indeed, the observed ineffectiveness of culling would seem likely to enhance perturbation effects (although the relationship between culling efficiency and magnitude of perturbation remains unknown).

3.6.2. Survey-only control
Where no badgers are killed, the prediction is that perturbation will gradually diminish, and with it will diminish contacts of an appropriate type to lead to disease transmission. As a general rule we have demonstrated that a badger population, as at North Nibley, can take five years to recover numerically, and even then it had not achieved the spatial organisation of undisturbed populations to which, after some further years, it might be predicted to converge (assuming similar conditions of habitat and resources). Within the TEE treatment population, measures of social disruption within the Other groups tended to decline over the course of the study and their demography remained consistent. These groups would not have been subjected to culling for at least four years (since 1998) and in most cases longer. A logical possibility is that the new prevalence to which a population might move after the repair of perturbation may be higher than would have been the case if perturbation had never occurred. Thus, to the extent that perturbation does underlie the failure of control and the worsening of the situation, previous attempts at control may have created a situation that makes a future solution less likely than would have been the case if they had never been attempted.

3.6.3. Pro-active treatment
Because we predict that the magnitude of the perturbation effects will depend on the size of the area culled and (not necessarily straightforwardly) on the effectiveness of the culling, and because the proactive treatments are 100 sq. km, we might expect this large size to diminish the counter-productive effect of perturbation within. However, while the area to perimeter geometry gives larger areas relatively shorter perimeters, the fringe of perimeter farms around a larger area includes, in absolute terms, a larger acreage of farms (although for a given total area of culling, there will be fewer perimeter farmers the larger each cull zone is). While their colleagues at the centre of the control area have the best chance of avoiding perturbation effects, the perimeter farmers are predicted to be most likely to face perturbation effects. Indeed, Donnelly et al. (2005) reveal that cattle bTB incidence rates increased at the periphery of Proactive zones, but decreased within the zone. Furthermore, Woodroffe et al. (2006) found that badger social group ranges increased amongst survivors within reactive and proactive culling areas and along the perimeters outside of proactive culling areas. Their finding, at a large scale, accords so closely with our observations of individual and group behaviour at North Nibley and in the TEE, and with those of Cheeseman et al. (1993) and O’Corry-Crowe et al. (1996), that the combined circumstantial evidence is strong that perturbation of badgers is an important causal mechanism limiting the usefulness of badger culling as a means of controlling bTB in cattle.

So, should badger culling be a part of Britain’s strategy, under current circumstances, to control bTB in cattle? The answer is no, because the evidence to date shows that unless culling was to be carried out over very large areas (probably substantially greater than 100 sq. km), and in ways that are
more effective than has proven possible in past culls, there
will at best be little benefit. This is due to the demonstrated in-
crease in cattle TB incidence at the edges of control areas, and
the likelihood of similar counter-productive effects within culled areas wherever there are gaps or inefficiencies (both of
which, on past evidence, are inevitable). The likely reason
for this is the perturbation effect (changes in the movements,
social behaviour and possibly immunity of surviving badgers).
Whatever the mechanism, the evidence is that any badger cull
carried out in a similar way to it predecessors is unlikely to de-
crease significantly the incidence of bTB in cattle, and may
well make it worse – this at a great cost, financially, in public
discord and to badgers. The evidence is that any badger cull
on a scale or level of efficiency that seems feasible will not
solve the cattle farmers’ problem – that problem is truly seri-
ous, and understandably the feeling is that something must
be done, but the evidence is that it should not be a badger cull.

4. Discussion

4.1. Other species hypothesis

Our results suggest that the prevalence of infectious individ-
uals is likely to be very low for most non-badger farmland
wildlife species in the UK. Average numbers of animals
trapped, and the distribution of species, were similar on case
and control farms, therefore underestimation of prevalence
due to ‘over-sampling’ of control farms (where prevalences
might have been expected to be lower) seems unlikely. Occa-
ional spill-overs into wildlife populations from badgers and
cattle may occur: the same strain was detected in a badger,
bank vole and cow on the same farm. Nevertheless, modelling
suggests that even the most ubiquitous of farmland rodents
and lagomorphs is unlikely to play an important role in the
epidemiology of bTB in cattle. Foxes, which have been the
subject of much previous research (Krebs et al., 1997),
are similarly unlikely to be important reservoirs due to their
low density and low infection prevalence. It is difficult to ob-
tain good prevalence estimates for bTB in non-badger muste-
lids, so a possible role for these species cannot be ruled out.
It is possible that deer, which were the focus of a sister study at
CSL (Delahay et al., in press), may sometimes play a role in
bTB epidemiology where densities are high and where deer
and cattle share forage. Delahay et al. (in press) emphasise
that the role of fallow deer, Dama dama, merits further study.
Deer in the UK have been found to be infectious for M. bovis
(Krebs et al., 1997) with a prevalence of around 1–2%, and
there is evidence from other countries of transmission be-
tween deer and cattle (Schmitt et al., 2002; Wilkins et al.,
2003; Aranaz et al., 2004). However, the prevalences observed
in the UK, together with the patchy distribution of deer, sug-
gests that their importance is likely to be localised. We con-
clude that if any wildlife species plays a significant role in the
epidemiology of bTB in cattle, it is likely to be badgers.

4.2. Perturbation hypothesis

Returning to the three questions posed at the outset, our
studies have demonstrated that badger culls perturb the
behavioural ecology of survivors’ and we have evidence, that
perturbation increases incidence of bTB in badgers, especially
in groups close to those that are removed. Furthermore, the
comparison between patterns of infection in culled popula-
tions and those published by Delahay et al. (2000) for an
undisturbed population may indicate that the perturbation
associated with control can cause the spatial distribution of
bTB in badgers to change from one in which it is contained
within spatially discrete pockets of high prevalence to one
where it is more widely, if thinly, spread. This could affect
meta-population dynamics of the disease; for example per-
turbation may encourage re-infection of patches where the
disease has naturally become extinct – thereby increasing
the persistence of the disease.

4.2.1. Efficacy of badger removal operations

Our two case studies present two different situations. First, at
North Nibley the then Ministry of Agriculture Food and Fish-
eries (MAFF – to become Defra in 2001) field staff targeted
sets that we knew to be occupied by four ELISA-positive bad-
gers and one culture-positive badger. They removed all bad-
gers from most of the sets, including all known positive
badgers. Before the cull, the prevalence in this area had been
low and localised for ELISA-positive badgers, and extremely
low for infectious badgers. Following the cull no positive bad-
gers of any type were detected for four years. Second, in the
TEE treatment area E1, the government’s field staff targeted
an area that included 21 sets we knew to be occupied by
six culture-positive badgers, of which they caught only one;
this left 47 badgers, including five known to be culture posi-
tive in occupancy. Furthermore, we knew of 29 additional cul-
ture-positive badgers, living in 19 sets alongside a further 299
culture-negative badgers that more or less closely adjoined
the removed groups. The situation described for TEE treat-
ment area is probably more typical; Bourne et al. (2005) sug-
gest that follow-up captures an average of 16 months after
the original culls in reactive areas were about 85% of the ori-

ginal numbers culled. At a broader scale, Woodroffe et al.
(2006) provide evidence that after culling there were fewer
badgers in RBCT Reactive zones than in Survey-only zones,
and fewest of all in Proactive zones – it would have been per-
plexing if it had been otherwise but it remains the case that
within proactive zones “badger populations appear to have
persisted nonetheless, with a proportion of sets showing high
levels of activity”. Government officials were not given
permission to cull badgers on 21% of the land area in proac-
tive treatment zones (Bourne et al., 2005).

In North Nibley, and the treatment and control areas of
Triplet E, herd breakdowns continued following BROS. In
North Nibley there were two breakdowns in four years, both
apparently in the absence of any positive badgers. In the
TEE treatment area two breakdowns in one year occurred in
areas where no positive badgers were known, and in the con-
trol area, one breakdown occurred in a region where bTB
prevalence in the badger population increased throughout
the study.

4.2.2. Perturbation as a consideration in planning future bTB
control in cattle

Three practical questions face those thinking about whether
culling badgers is currently a sensible option for the control
of bTB in cattle. How efficient would a cull need to be, over what area should it be implemented, and over what time scale should it be continued? The answers are doubtless linked.

Regarding efficiency, we have seen that the best efforts of government officials under the circumstances of the RBCT resulted in a cull of 35–44% of badgers in the TEE treatment population, and perhaps more in the Proactive areas. Neither was sufficient, within treatment blocks of up to 100 km², respectively, to achieve a substantial result (the best outcome being the 19% reduction in prevalence in cattle in the core of proactive zones). It is possible that in the circumstances of lowland England it is not feasible to improve on this level of efficiency. Furthermore, it is also not clear that an improvement in efficiency of badger killing would lead to a pro rata reduction in bTB either in badgers or cattle (a somewhat more efficient cull might produce even greater perturbation). In this context, it may be simplistic to urge field staff to try harder and be more efficient. The difficulties of trapping unhabituated (already perturbed and potentially trap-shy) badger populations (Tuyttens et al., 1999), the availability and calibre of staff, the working practices to which they are subject, and the effects of seasonality, legislation, farmer-cooperation, are just some of the factors that might make it a delusion to believe that effectiveness can be radically improved.

Turning to the size of culled areas, we predict that the perturbation effect will be scale dependent, and at very large scales it will be progressively less relevant. From how big an area must badgers be removed in order for the perturbation effect to be unimportant? Our findings at from the TEE suggest that removing badgers from an area of about 20 km², at the efficiency hitherto achievable by government officials, was insufficient to control the disease in badgers, and may have made it worse. However, there is historical evidence that very intensive killing of badgers at Hartland in North Devon (62 km²) and Thornbury in Avon (104 km²) was associated with lowered prevalence in cattle (Clifton-Hadley et al., 1995b), as was the removal of badgers from East Offaly (738 km²) (O‘Mairein et al., 1998) and four 245 km² sites in Ireland (Griffin et al., 2005). A plausible conclusion is that removal areas would have to be larger than 100 km², and one analysis is that the threshold where the positive influence of culling starts to outweigh the negative was around 154 km² (Donnelly et al., 2005; C. Donnelly, Pers. Commun.).

In this context the findings of the Irish 4-Area Badger Culling Study assume particular importance. Few details about the badger populations and their bTB status are presented by Griffin et al. (2005) for the Irish 4-Area Study, but they compared a total of 1214 km² from which 1113 badgers were removed in the first year (0.92 badgers removed per km²), with reference areas in which reactive culling was practiced (a treatment associated elsewhere with worsening of bTB in cattle). Overall, after five years of study, bTB prevalences in badgers were 19.5% (n = 2310) in the removal areas and 26.1% in the reference areas (n = 218), and an effect in cattle became apparent after 2–3 years. By the fifth year the rate of herd breakdowns in cattle in the removal areas fell by 60–96% compared with reference areas. It would, however, be impudent to extrapolate to the conclusion that killing badgers from areas of c. 245 km² (c. 16 × 16 km) would lead to a comparable reduction in herd breakdowns in SW England, because there are differences in biological, logistical and political circumstances. By comparison, the proactive treatment in the RBCT used cage traps (not snares), had lower landowner participation, faced significant disruption from animal activist groups, did not trap during the badger breeding season, released lactating females, and during the first year removed between approximately 1.7–6.0 badgers per km² (average = 3.4). Reasons for doubting that the Irish approach would work in lowland England include that in Ireland the badger densities started much lower, the removal areas were deliberately geographically isolated (for example, in some cases by coastline), had high levels of farmer and public compliance, were highly rural, with few substantial human settlements, and thus different risk factors for a by-catch of domestic pets and different attitudes to public access. It is sometimes argued that a future badger cull in England could be more effective than was the RBCT because the latter was hampered by, for constraints such as concerns about animal welfare and by non-compliance. However, we can see no reason why such constraints should be less in the future. Ultimately, the issue of how big an area would need to be culled will be affected by judgment as to what level of control justifies a given policy.

The third practical question is for how long should badgers be culled in removal areas. Following one cull badgers will recolonise and, all else being equal, reintroduce bTB (perhaps exacerbated by perturbation). Of course, all else may not be equal – in the meantime a new invention (perhaps vaccination) might change everything; otherwise, the political (and other) implications of allowing badgers to recolonise will create problems that may have wide repercussions, as may relations between farmers at the centre of removal areas and those at the (perturbed) perimeter.

5. Conclusion

Studies of badger biology, and epizootiological models of the transmission of bTB amongst badgers and between badgers and cattle, are essential to inform policy. For example, the effects of perturbation provide one possible explanation of the failure of badger control as a means of reducing bTB in cattle, and may also provide one explanation for why prevalence in both badgers and cattle has increased. To have any prospect of achieving a better result than previous culls an approach would have to be devised that overcomes the counter-productive edge-effect, that avoids gaps (due, for example, to lack of compliance), deals with complicated unknowns relating efficiency to effectiveness, adopts a killing method that is acceptable on welfare grounds to the public, is not compromised by the interventions of objectors, and which could be implemented and coordinated over very large areas. Finally it will need an open-ended commitment spanning the years until a (perturbation-free) exit strategy allowed it to be replaced by an as yet unknown alternative solution. However, even if these problems could be solved, the next steps go beyond the realms of biology. First, it will then be necessary to estimate the full economic cost of removing badgers from that area. For example, comparisons can be made of removing badgers once, or repeatedly and indefinitely, or for any intermediate period. These costs would then need to be compared
to the benefits to cattle farming, evaluated within the rapidly changing context of new agri-environment payments (see Smith et al., 2006). Insofar as the tax-payer is the source of farm payments, and considering that these payments are now made not for production but for custody of the countryside, tax-payers will surely have a view on whether or not they wish to pay for removing badgers from large areas, especially in the absence of evidence that this will reduce substantially the problem of bTB in cattle. Indeed, a full cost benefit analysis would have to extend beyond the killing of badgers and the farming of cattle to consider also all the societal choices involved. For example, against the background of reformed farm payments for biodiversity gains, is it appropriate national policy to prioritise keeping cattle in areas where there is apparently endemic zoonotic disease? This question is phrased in a new climate which shifts land managers from consumers to the suppliers of what society wants of the countryside. Considering that cattle-to-cattle transmission is likely to be a very important component in the persistence of bTB in cattle, is society content to take the decision to prioritise livestock over biodiversity before a comprehensive programme to minimise cattle-to-cattle transmission has been exhaustively explored?

Government initiated the RBCT and related research to foster the principle of underpinning policy with science. If the findings were ignored, that principle would be undermined, raising interesting questions if, in consequence, farms adjoining some future badger cull were to suffer, as predicted, a bTB breakdown attributable to perturbation. The failure of badger control suggests that substantial parts of both the problem and the solution must be sought elsewhere, most promisingly in cattle movement controls, improved surveillance and cattle testing and animal husbandry. Alternative strategies include the long-awaited vaccination of cattle and/or badgers (e.g. Swinton et al., 1997), and the management of environmental conditions associated with the appearance of the disease in cattle (Mathews et al., 2006b). It is noteworthy that the kind of farmland habitat management associated with reduced risk of bTB in cattle (hedgerow buffer strips; good hedgerow management, etc.) is the same as that encouraged by agri-environment schemes. These valuable sources of income may therefore not only deliver benefits to wildlife, but also improvements in cattle health. In monetised terms, a judgment has to be made on whether the financial commitment to badger culling is justified by its impact on agricultural profitability. However, monetized terms will not be the only values to be taken into account.

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