The effects of annual widespread badger culls on cattle tuberculosis following the cessation of culling

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Summary

Background

The effective control of human and livestock diseases is challenging where infection persists in wildlife populations. The Randomised Badger Culling Trial (RBCT) demonstrated that, while it was underway, proactive badger (*Meles meles*) culling reduced bovine tuberculosis (TB) incidence inside culled areas but increased incidence in neighboring areas, suggesting that the costs of such culling might outweigh the benefits.

Objectives and design

The objective of this study was to investigate whether culling impacts persisted more than one year following the cessation of culling (the 'post-trial' period). We compared TB incidence in and around RBCT proactive culling areas with that in and around matched unculled areas.

Results

: During the post-trial period, cattle TB incidence inside culled areas was reduced, to an extent significantly greater ($p = 0.002$) than during culling. In neighboring areas, elevated risks observed during culling were not observed post-trial ($p = 0.038$). However, the post-trial effects were comparable to those observed towards the end of the trial (inside RBCT areas: $p = 0.18$ and neighboring areas: $p = 0.14$).

Conclusions

Although to-date the overall benefits of culling remain modest, they were greater than was apparent during the culling period alone. Continued monitoring will demonstrate how long beneficial effects last, indicating the overall capacity of such culling to reduce cattle TB incidence.

Keywords: Bovine TB; *Mycobacterium bovis*; Badger culling; Cattle

Article Outline

Introduction

The effective control of human and livestock diseases is challenging where infection persists in wildlife populations. The Randomised Badger Culling Trial (RBCT)[1] demonstrated that, while it was underway, proactive badger (*Meles meles*) culling reduced bovine tuberculosis (TB) incidence inside culled areas but increased incidence in neighboring areas,[2], [3], [4] and [5] suggesting that the costs of such culling might outweigh the benefits.[1], [6] and [7]

Bovine tuberculosis (TB), a serious disease of cattle, was eliminated from most of Britain by 1960, when the whole country was declared attested, using a policy of routine testing of cattle combined with slaughter of affected animals.[8] However, infection remained in areas of southwest England, where it was linked to infection of local badger (*Meles meles*, Figure 1) populations with *Mycobacterium bovis*, the causative agent of the disease.[9] Since 1979 incidence in British cattle has increased and the infection has become more geographically widespread.[10] This increase has occurred despite badger culling being an additional component of the British TB control policy from 1973 until the start of the RBCT in 1998.[10]

 Full-size image (146K)

Figure 1. European badgers (Meles meles). In populations undisturbed by culling, badgers are highly social; disruption of this social behaviour is thought to lead to expanded ranging, and increased disease transmission both among badgers and from badgers to cattle. Photos credited to Richard Yarnell.

The RBCT[1] was designed to evaluate the effectiveness of two badger culling strategies, by comparing the incidence of cattle TB under three experimental treatments—repeated widespread ('proactive') culling, localized ('reactive') culling, and no culling ('survey-only')—each replicated ten times in large (100 km^2) trial areas. Results from the RBCT published at the completion of the proactive strategy, after roughly five years of annual culling,[2] and [3] showed that proactive culling reduced cattle TB incidence inside the culled areas. However, incidence was elevated in neighboring unculled areas (up to 2 km outside the culled areas). The latter effect apparently occurred because culling induced changes in badger behavior,[11] which increased the transmission of infection both between badgers,[12] and from badgers to cattle. Localized reactive culling as a once-only event in response to each herd breakdown, likewise was associated with an overall detrimental effect,[4] and [5] apparently for similar ecological reasons.[11] At the scale and over the period on which RBCT culling was conducted, the detrimental effects (24% increased incidence) observed outside proactive culling areas counteracted the benefits (23% reduced incidence) experienced inside; the relative magnitude of these effects would be expected to vary with the size of the area culled.[2] The evidence available at the end of the RBCT indicated that a circular culled area of at least 265 km^2 would be required to provide 95% confidence that the overall impact would, on average, be a net reduction in the incidence of confirmed herd breakdowns.[1]

There has been considerable debate about the importance of the detrimental effects associated with badger culling compared to the associated beneficial effects, observed while annual culling was ongoing.[13], [14], [15] and [16] Available data from the RBCT suggested that only modest reductions in confirmed herd breakdowns would be achievable by badger culling, even if large areas were culled, repeatedly, systematically, and simultaneously (and hence at substantial cost), while small-scale, short-term, or patchy culling was expected to make matters worse; this called into question whether badger culling could meaningfully contribute to the control of cattle TB in Britain.[1] Stakeholders made clear their strongly held and diverse (often directly opposing) views on the form of future TB control policy[17], [18] and [19] in a public consultation on badger culling,[20] which followed the first publication of results of proactive culling within the RBCT:[3] the consultation received more than 47 000 replies,[21] reflecting the level of public concern in the badger culling issue.

The utility of badger culling as a TB control measure will be influenced not only by the magnitude of its beneficial and detrimental effects, but also by their persistence. The last proactive culls occurred in 2005, but monitoring of cattle TB incidence has continued in and around all trial areas as part of routine TB surveillance. We therefore compared cattle TB incidence in and around proactively culled areas with that in and around survey-only areas, to determine whether the effects of proactive culling observed during the RBCT persisted following the cessation of culling. We also re-evaluated whether the size of the culled area required to achieve an overall net reduction in the incidence of confirmed herd breakdowns has changed in light of the additional data.

Materials and methods

Trial design

Thirty trial areas, selected on the basis of high cattle TB incidence, were recruited sequentially as 10 matched 'triplets' denoted A–J (see supplementary material for map). Nearby trial areas were separated by at least 3 km. Each trial area was surveyed for badger activity and then randomly allocated to treatments (except in triplet I, for which security concerns directed a specific allocation) such that each treatment—proactive culling, reactive culling, or no culling ('survey only')—was repeated once within each triplet.

Immediately following treatment allocation, initial proactive culls were conducted on all land for which landholder consent was obtained (see supplementary material for data on proportion of proactive trial area land for which consent was obtained; note that analyses show that the culling methods used were successful in removing badgers from land for which no access was obtained[2]). The boundaries of the areas to be culled were delineated (beyond trial area boundaries as necessary) using field survey data to ensure that culling targeted the home ranges of all badgers likely to use farms inside the trial areas; where possible, culling area boundaries followed likely geographical barriers to badger immigration. Badgers were captured in cage traps placed primarily at setts, with no trapping between 1 February and 30 April each year, to avoid killing mothers with dependent cubs below ground.[22] Few badgers were found to have trap-related injuries[23] and [24] and badger killing (by gunshot) was deemed 'humane' by independent audit.[25]

Initial culls for each proactive trial area were completed between December 1998 and December 2002, with 'follow-up' culls repeated approximately annually (with longer delays in seven areas incurred due to a nationwide epidemic of foot-and-mouth disease in 2001). The final culls for all 10 proactive areas were completed between May and October 2005. Field surveys indicated that badger activity in trial areas changed according to the culling treatment received,[26] with no evidence that treatment comparisons were substantially compromised by illegal culling in survey-only areas.

Once each initial proactive cull was complete, cattle TB incidence inside, and up to 2 km outside, each trial area was monitored using established veterinary surveillance. Effects were sought up to 2 km outside trial areas because culling had been shown to influence badger numbers and movement patterns on this spatial scale.[11] The 'during-trial period' was defined as the period from the completion of the initial proactive cull in each triplet, to exactly one year after completion of the last cull in each triplet, when another annual cull would have been conducted had the proactive treatment been continued. The subsequent time period was termed the 'post-trial period'. Data were available until 6 January 2008, and consisted of accrued totals from 55.7 'triplet-years' in the during-trial period and 14.3 'triplet-years' in the post-trial period (where a 'triplet-year' is one triplet observed for 12 consecutive months). Analyses were restricted to 'confirmed breakdowns' (incidents in which post mortem examination of slaughtered cattle led to detection of TB lesions or culture of *M. bovis*); some breakdowns detected in late 2007 would not have been confirmed in time to be included in these analyses.

Statistical analysis

As in previously published analyses,[2], [3], [4] and [5] we used log-linear Poisson regression to compare the numbers of confirmed breakdowns recorded in and around trial areas subjected to the proactive and survey-only treatments. The regression models adjusted for triplet, the log of the number of baseline herds at risk, and the log of the number of confirmed breakdowns recorded in a three-year period before RBCT culling. Where results were stratified by time, a triplet by time interaction term was also included in the model. Confidence intervals (CI) and *p*-values were conservatively adjusted for extra-Poisson overdispersion by using an adjustment factor (the square root of the model deviance divided by the degrees of freedom) in all cases where its value was greater than 1. We used a Chi-square test, summing confirmed herd breakdowns over triplets, to look for any difference between the effect of proactive culling on the incidence of confirmed herd breakdown observed in the last two years of the during-trial period and that observed in the first year post-trial.

Cattle herd locations from the national animal health information system VetNet were used to identify herds inside trial areas. Parallel analyses were performed using the RBCT database to identify herd locations; the results obtained were similar but less consistent (see supplementary material). Herds up to 2 km outside trial area boundaries were identified more comprehensively using VetNet, because the RBCT database did not include all farms on neighboring land. Any herds within 2 km of more than one trial area boundary (whether proactive, reactive, or survey-only) were omitted from these analyses. Analyses based on VetNet herd locations include 2659 herds inside trial areas and 2262 herds in neighboring areas, up to 2 km outside trial area boundaries (proactive and survey-only areas combined).

As in previously published analyses,[1] we attempted to estimate the area of land that would need to be targeted by culling to obtain an overall reduction in the incidence of confirmed herd breakdowns (with detrimental effects outside the culled area offset by benefit effects inside). To do this, we investigated whether the effect of culling varied with distance from the trial area boundary, combining the data from the during- and post-trial periods. Any change in effect with distance would have implications for extrapolation to areas larger or smaller than the 100 km^2 used in the RBCT. Tests for trends in culling effects, with distance from the trial area boundary, were undertaken using weighted least squares on the estimated logarithms of the relative risks associated with each distance category (0–1, 1–2, 2–3, 3–4, and >4 km inside the trial area boundaries or 0–0.5, 0.5–1, 1–1.5, and 1.5–2 km outside the trial area boundaries). These estimates were obtained from models fitted simultaneously to data from distance categories inside the trial area boundaries (with negligible correlation between estimates of effects associated with different distance categories – see supplementary material), and in a separate model to the data from distance categories outside the trial area boundaries.

Results

Analyses revealed that, during the post-trial period, the incidence of confirmed cattle herd breakdowns was 54% lower inside proactive trial areas than inside survey-only areas ($p < 0.001$ for the null hypothesis of no effect; 95% confidence interval (CI): 39–66% reduction; Table 1, Figure 2). This result was consistent across all ten triplets (the test for overdispersion was not significant, $p = 0.76$). However, this effect in the post-trial period was substantially greater than that observed in the during-trial period (23% reduction (95% CI: 12–33% reduction),[2] $p = 0.002$ for the null hypothesis of the same effect in the during- and post-trial periods). There was no evidence of a difference between the effect in the latter part of the trial (last two years during-trial) and the first year of the post-trial period ($p = 0.18$). Pooling results over the whole time period (during- and post-trial) showed that incidence was reduced by 30% (95% CI: 21–38% reduction); however, this estimate hides the significant improvement in the impact of proactive culling on the incidence of confirmed cattle herd breakdowns inside proactive trial areas.

Table 1. Estimated effects of proactive culling on the incidence of confirmed cattle TB breakdowns inside trial areas

	Proactive effect			**Overdispersion**	
	Estimate	**95% CI**	***p*-Value**	**Factor**	***p*-Value**
1st to 2nd cull	−3.6%	−33.1 to 38.9%	0.85		
2nd to 3rd cull	−12.9%	−38.8 to 24.2%	0.45		
3rd to 4th cull	−39.6%	−59.3 to −10.3%	0.013	1.33	0.001
After 4th cull to end of during-trial period	−31.8%	−48.5 to −9.7%	0.007		
First year of post-trial period	−48.7%	−65.6 to −23.2%	0.001		
Second year of post-trial period	−60.8%	−80.7 to −20.5%	0.009		
All during-trial period combined	−23.2%	−32.7 to −12.4%	<0.001	0.67	0.87
All post-trial period combined (1st and 2nd year combined)	−54.4%	−66.2 to −38.5%	<0.001	0.77	0.76
1st cull to 6 January 2008	−30.2%	−38.1 to −21.3%	<0.001	0.73	0.81

95% CI, 95% confidence interval.

Analyses adjust for triplet, baseline number of herds, and historic TB incidence (over three years). Results are split by cull sequence during-trial and by year post-trial and include breakdowns from the initial cull to 6 January 2008. During-trial results include all confirmed breakdowns in the period from completion of the initial proactive cull (in each triplet) to one year after the last proactive cull (in each triplet) and use the January 2007 data download as reported in the ISG Final Report. The post-trial results include all reported confirmed breakdowns from one year after the last proactive cull (in each triplet) to 6 January 2008 and use the download from 6 January 2008. All results are based on locations from the VetNet database.

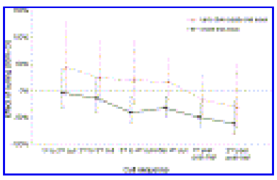
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Figure 2. Estimated effects of proactive culling on the incidence of confirmed cattle TB breakdowns inside trial areas and up to 2 km outside trial area boundaries. The estimated effects of proactive culling are stratified by time periods defined by the timings of the culls during the trial, and by year from 1 year after the last proactive cull (post-trial period). The black line shows the effects inside the trial areas and the dotted red line shows the effects in the neighboring areas. These figures are also shown in Table 1 and Table 2.

On land neighboring proactive trial areas, no detrimental effects were observed in the post-trial period: the incidence of confirmed cattle herd breakdowns was 23% lower (95% CI: 44% lower to 7.3% greater) than that on land neighboring survey-only trial areas (*p* = 0.12 for the null hypothesis of no effect; the test for overdispersion was not significant showing that the effect was consistent across all 10 triplets, *p* = 0.56; Table 2, Figure 2). However, again, the effect in the post-trial period was significantly different from the detrimental effect (24% greater incidence (95% CI: 1% lower to 56% greater)) observed in the during-trial period (Figure 2, *p* = 0.038 for the null hypothesis of the same effect in the during- and post-trial periods). As with inside trial areas, there was no evidence of a difference between the effect in the latter part of the trial (last two years during-trial) and the first year of the post-trial period (*p* = 0.14 for neighboring areas). Pooling results over the whole time period (during- and post-trial) showed that incidence was increased by 13% (95% CI: 8% reduction to 38% increase); however, this estimate hides the significant improvement in the impact of proactive culling on the incidence of confirmed cattle herd breakdowns on land neighboring proactive trial areas.

Table 2. Estimated effects of proactive culling on the incidence of confirmed cattle TB breakdowns up to 2 km outside the trial area boundaries

	Proactive effect			Overdispersion	
	Estimate	95% CI	*p*-Value	Factor	*p*-Value
1st to 2nd cull	43.9%	−8.6 to 126.7%	0.12		
2nd to 3rd cull	24.4%	−19.0 to 91.0%	0.32		
3rd to 4th cull	20.0%	−25.0 to 92.1%	0.45	1.25	0.007
After 4th cull to end of during-trial period	17.3%	−14.4 to 60.9%	0.32		
First year of post-trial period	−16.2%	−45.4 to 28.9%	0.42		
Second year of post-trial period	−30.1%	−67.3 to 49.2%	0.35		
All during-trial period combined	24.5%	−0.6 to 56.0%	0.057	1.26	0.13
All post-trial period combined (1st and 2nd year combined)	−22.7%	−44.3 to 7.3%	0.12	0.91	0.56
1st cull to 6 January 2008	12.5%	−8.5 to 38.3%	0.27	1.33	0.091

95% CI, 95% confidence interval.

Analyses adjust for triplet, number of baseline herds, and historic TB incidence (over three years). Results are split by cull sequence during-trial and by year post-trial and include breakdowns from the initial cull to 6 January 2008. During-trial results include all confirmed breakdowns in the period from completion of the initial proactive cull (in each triplet) to one year after the last proactive cull (in each triplet) and use the January 2007 data download as reported in the ISG Final Report. The post-trial results include all reported confirmed breakdowns from one year after the last proactive cull (in each triplet) to 6 January 2008 and use the download from 6 January 2008. All results are based on locations from the VetNet database.

We used these results to predict the effects of culling targeted at areas of different sizes assuming a herd density of 1.25 per km^2 (roughly that seen in the RBCT areas) and an incidence rate in the absence of culling of eight confirmed breakdowns per 100 herds per annum (a reasonable approximation based on data from the survey-only areas during the RBCT). For example, five annual proactive culls targeting a circular area of 125 km^2 would be predicted to prevent, on average, only roughly three confirmed breakdowns (14.5 prevented within the 125 km^2 targeted area and 11.2 induced in the 92 km^2 neighboring area) in the during-trial period. An additional roughly nine confirmed breakdowns would then be prevented, on average, in the following 12 months (6.8 prevented within the targeted area and 2.1 prevented in the neighboring area). Combining the results from these two time periods gives roughly 12 fewer confirmed breakdowns predicted, on average, in a six-year period including five annual proactive culls with culling then discontinued. For comparison, in the absence of culling 130 confirmed breakdowns would have been expected in the affected area (125 km^2 targeted plus 92 km^2 neighboring) over the same six-year time period.

Over the whole time period (during- and post-trial combined), there was a non-significant trend for the benefits of culling to increase as one moves deeper inside trial area boundaries ($p = 0.083$; Table 3); this was expected as more thorough badger removal was achieved deep inside trial areas.[26] There was no evidence of a trend for the effects of culling to change with distance outside the trial area boundary ($p = 0.46$; Table 3). In extrapolating to areas of different sizes, we therefore assumed that the beneficial effects of proactive culling inside targeted areas varied with the distance from the boundary, while the detrimental effect on neighboring lands was constant. On this basis, across the combined during- and post-trial periods (including typically five annual proactive culls with culling then discontinued), and considering effects both inside and outside the targeted area, the overall average effect of proactive culling was predicted to lead to a net reduction in the overall incidence of confirmed herd breakdowns, considering the whole affected area, when targeted at circular areas larger than 29 km^2 (Figure 3). However, the 95% CI for the average effect across the entire affected area only excluded net increases in the overall incidence of confirmed herd breakdowns, again considering the whole affected area, for culling targeted at circular areas of 119 km^2 or more. If assumptions were modified so that the treatment effect was constant across the targeted area, the 95% CI excluded net increases in the overall incidence of confirmed herd breakdowns for circular areas of 110 km^2 or more (see supplementary material).

Table 3. Estimated effects of proactive culling on the incidence of confirmed cattle TB breakdowns inside trial areas and up to 2 km outside trial areas

	Proactive effect			**Overdispersion**		***p*-Value for linear trend**
	Estimate	**95% CI**	***p*-Value**	**Factor**	***p*-Value**	
Inside treatment areas						
0–1 km inside	−19.5%	−35.4 to 0.3%	0.053			
1–2 km inside	−22.1%	−40.8 to 2.5%	0.074			
2–3 km inside	−36.3%	−55.0 to −9.9%	0.011	1.33	<0.001	0.083
3–4 km inside	−28.9%	−58.0 to 20.2%	0.20			
4–5 km inside	−53.5%	−87.7 to 75.8%	0.26			
Outside trial areas and within 2 km of the trial areas						
0–0.5 km outside[a]	−18.6%	−38.6 to 7.8%	0.15			
0.5–1 km outside	28.0%	−3.0 to 68.8%	0.081	1.08	0.18	0.46
1–1.5 km outside	1.6%	−25.0 to 37.6%	0.92			
1.5–2 outside	16.7%	−16.8 to 63.7%	0.37			

95% CI, 95% confidence interval.

Analyses adjust for triplet, number of baseline herds, and historic TB incidence (over three years). Results are split by distance from the trial area boundary and include breakdowns from the initial cull to 6 January 2008. During-trial results include all confirmed breakdowns in the period from completion of the initial proactive cull (in each triplet) to one year after the last proactive cull (in each triplet) and use the January 2007 data download as reported in the ISG Final Report. The post-trial results include all reported confirmed breakdowns from one year after the last proactive cull (in each triplet) to 6 January 2008 and use the download from 6 January 2008. All results are based on locations from the VetNet database.

[a] Treatment areas, within which culling was conducted, were slightly larger than trial areas, and were delineated according to the estimated boundaries of social group territories so that all badgers using farms inside the trial areas could be targeted. As a consequence, some culling was conducted on land immediately outside trial area boundaries (see supplementary material for parallel analyses).

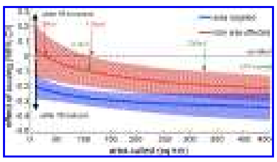
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Figure 3. Effects of varying the size of the area targeted for badger culling on the projected impacts on confirmed cattle TB incidence. Red shading shows the 95% confidence interval for the overall impact (combining impacts inside and up to 2 km outside the targeted area) of culling targeted at circular areas of different sizes; blue shading shows the impact inside the targeted area only. The estimated overall effect is for increased incidence when culling targets areas less than 29 km^2, moving to a decreased incidence when areas of more than 29 km^2 are targeted. The effect of decreased overall incidence is statistically significant for areas over 119 km^2. Likewise, on average culling is expected to lead to an overall reduction in cattle TB incidence of ≥10% if targeted at areas larger than 111 km^2, with the expected reduction significantly greater than 10% for areas over 330 km^2. Calculations assume a trend with distance going deeper inside the trial area from the trial area boundary. To avoid extrapolation beyond the available data, when the beneficial effects of culling are assumed to be linearly dependent on the distance from the boundary, the effect on land more than 4 km inside the trial boundary was assumed to equal to that estimated for such land in the roughly 100 km^2 RBCT trial areas, even though for much larger culling areas some land will be much further than 4 km from the nearest boundary.

For comparison, we also investigated the size of the area at which culling would need to be targeted to achieve an overall reduction in the incidence of confirmed herd breakdowns (considering effects both inside and outside the targeted area) of 10% or more. On average, such benefits could be expected if culling were targeted at circular areas larger than 111 km^2 (see Figure 3). However, the 95% CI around this average value only excluded benefits of <10% for culling targeted at circular areas of 330 km^2 or more (Figure 3). If assumptions were modified so that the treatment effect was constant across the targeted area, the 95% CI excluded benefits of <10% for circular areas of 443 km^2 or more (see supplementary material).

Discussion

Our results show that the reductions in cattle TB incidence achieved through proactive badger culling, as conducted in the RBCT, persisted for more than one year after culling was discontinued. Beneficial effects inside culling areas increased in magnitude, and detrimental effects were no longer observed on neighboring lands.

The epidemiological mechanisms causing this increase in the beneficial effects of badger culling are uncertain. This is unfortunate, because an insight into these mechanisms would help to predict how long the benefits might be expected to persist.

On the basis of available data, we speculate that the changes observed in cattle TB risks following the cessation of culling reflect changes in the behavior and ecology of badgers, noting that these changes in the risks to cattle were non-significant compared with the final two years of the during-trial period. In the during-trial period, proactive culling was shown to have caused a substantial reduction in badger density inside culled areas, and a smaller reduction on neighboring unculled lands.[11] and [26] In both types of area, badgers ranged more widely;[11] the consequently greater opportunities for each infected badger to come into contact with cattle was thought to have caused the detrimental effects on cattle TB outside culling areas, and also to have undermined the beneficial effects inside.[3] This expanded ranging behavior also promoted opportunities for transmission among badgers, and probably explains the greater prevalence of *M. bovis* infection observed in badgers on successive culls, which would have further undermined the benefits of reduced badger density.[12]

The subsequent cessation of RBCT culling is likely to have had several consequences for the badger population. It would allow the population to grow, as the abundant, unexploited food source available for badgers would allow high reproductive rates and cub survival.[27] and [28] In addition, a stable social organization would be re-established, leading to contraction of home ranges and greatly reduced immigration.[29] These two aspects of badger population recovery are likely to occur at different speeds, with changes in badger behavior occurring more rapidly than changes in badger numbers: at two removal sites previously studied in Gloucestershire, badger ranging behavior contracted markedly within two years, but it took 10 years for the original badger densities to be re-established.[29] These two effects would have contrasting implications for the incidence of cattle TB: growth of the badger population would be expected to increase the risks of cattle becoming infected from badgers, while the reduction in badger mobility would reduce those risks. We suspect that the reductions in confirmed herd breakdowns recorded in and around proactive areas following the suspension of culling, noting that these estimates were non-significantly different from those observed in the final two years of the during-trial period, reflect contractions in badger ranging at a time when badger numbers were still suppressed by past culling. If this explanation is correct, it suggests that the benefits observed in the first years post-culling will dissipate as badger numbers increase. Continued monitoring will allow testing of this prediction; the timescale on which benefits would be expected to disappear cannot yet be determined. It is likewise not possible to predict how culling over different periods of time, or at different intervals, would have influenced the results, since the outcome would depend upon a complex array of factors including badger movements, dispersal, reproduction, and trappability, all of which are likely to have changed in response to repeated culling as well as showing strong seasonal variation.

When considering the available data in their entirety, our analyses suggest that the overall reduction in the incidence of confirmed herd breakdowns associated with widespread badger culling remains modest (e.g., on average only 12 confirmed breakdowns prevented over six years by five annual culls targeting a 125 km^2 area, compared with 130 confirmed breakdowns expected in the absence of culling). As published previously, culling that is small-scale, patchy, or short-term is likely to increase, rather than reduce, TB risks to cattle.[1], [2], [3] and [5] In the during-trial period,[1] the 95% CI indicated that culling could be expected to lead to a net reduction in the overall incidence of confirmed herd breakdowns if targeted at circular areas greater than 265 km^2; the addition of data from the post-trial period reduced this minimum area to 119 km^2. While this area is considerably smaller than previously estimated, achievement of an effective cull across such an area would still require a coordinated and sustained effort; furthermore the economic costs of implementation (when considering the impact over the whole affected area) would exceed the savings achieved through reduced breakdown incidence (based on the estimated costs of performing culling and experiencing a breakdown[1] and [6]).

Our results suggest that the cessation of annual proactive badger culling influenced the dynamics of *M. bovis* infection in cattle and badgers. However, it must be stressed that these results refer only to the time course of badger culling that was implemented in the RBCT, within areas selected for inclusion in the RBCT based on their historic high TB incidence rates in cattle herds: no reliable predictions can be made concerning what would have happened had annual culling been continued for longer, or halted sooner. The reductions in confirmed herd breakdowns we describe from the post-trial period must be considered in the context of the smaller reduction (and indeed increased number of breakdowns in neighboring areas) observed when culling was ongoing. Continued monitoring will determine how long the beneficial effects last, and will thus provide a measure of the overall capacity of badger culling (as conducted in the RBCT) to reduce cattle TB incidence.

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Conflict of interest statement: HEJ and CAD have a research contract with the Department of Environment, Food and Rural Affairs (Defra) to analyze post-trial TB incidence data from cattle herds within RBCT areas. CAD and RW were formerly members of the Independent Scientific Group on Cattle TB (ISG) for which they received fees for time spent on ISG work and reimbursement of expenses from Defra. HEJ was formerly employed as a research assistant working with the ISG at Imperial College London.

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References

1 Bourne FJ, Donnelly CA, Cox DR, Gettinby G, McInerney JP, Morrison WI, et al. Bovine TB: the scientific evidence. Final report of the Independent Scientific Group on Cattle TB. London, UK: Defra; 2007. Available at: http://www.defra.gov.uk/animalh/tb/isg/pdf/final_report.pdf (accessed April 2008).

2 C.A. Donnelly, G. Wei, W.T. Johnston, D.R. Cox, R. Woodroffe and F.J. Bourne *et al.*, Impacts of widespread badger culling on cattle tuberculosis: concluding analyses from a large-scale field trial, *Int J Infect Dis* **11** (2007), pp. 300–308. **Article** | PDF (413 K) | View Record in Scopus | Cited By in Scopus (31)

3 C.A. Donnelly, R. Woodroffe, D.R. Cox, F.J. Bourne, C.L. Cheeseman and R.S. Clifton-Hadley *et al.*, Positive and negative effects of widespread badger culling on tuberculosis in cattle, *Nature* **439** (2006), pp. 843–846. View Record in Scopus | Cited By in Scopus (83)

4 Le Fevre AM, Bourne FJ, Donnelly CA, Cox DR, Gettinby G, McInerney JP, et al. The impact of localised reactive badger culling versus no culling on TB incidence in British cattle: a randomised trial. London, UK: Defra; 2005. Available at: http://www.defra.gov.uk/animalh/tb/isg/pdf/lefevre1005.pdf (accessed April 2008).

5 C.A. Donnelly, R. Woodroffe, D.R. Cox, J. Bourne, G. Gettinby and A.M. Le Fevre *et al.*, Impact of localized badger culling on tuberculosis incidence in British cattle, *Nature* **426** (2003), pp. 834–837. View Record in Scopus | Cited By in Scopus (109)

6 Defra. Cost benefit analysis of badger management as a component of bovine TB control in England. London, UK: Defra; 2005. Available at: http://www.defra.gov.uk/animalh/tb/pdf/badger_d.pdf (accessed April 2008).

7 I.D. Trewby, G.J. Wilson, R.J. Delahay, N. Walker, R. Young and J. Davison *et al.*, Experimental evidence of competitive release in sympatric carnivores, *Biol Lett* **4** (2008), pp. 170–172. View Record in Scopus | Cited By in Scopus (5)

8 A.J. Proud, Some lessons from the history of the eradication of bovine tuberculosis in Great Britain, *Government Veterinary Journal* **16** (2006), pp. 11–18.

9 C.L. Cheeseman, J.W. Wilesmith and F.A. Stuart, Tuberculosis: the disease and its epidemiology in the badger, a review, *Epidemiol Infect* **103** (1989), pp. 113–125. View Record in Scopus | Cited By in Scopus (54)

10 J.R. Krebs, R.M. Anderson, T. Clutton-Brock, W.I. Morrison, D. Young and C.A. Donnelly, Bovine tuberculosis in cattle and badgers. MAFF Publications, PB3423, MAFF, London, UK (1997).

11 R. Woodroffe, C.A. Donnelly, D.R. Cox, F.J. Bourne, C.L. Cheeseman and R.J. Delahay *et al.*, Effects of culling on badger *Meles meles* spatial organization: implications for the control of bovine tuberculosis, *J Appl Ecol* **43** (2006), pp. 1–10. View Record in Scopus | Cited By in Scopus (42)

12 R. Woodroffe, C.A. Donnelly, H.E. Jenkins, W.T. Johnston, D.R. Cox and F.J. Bourne *et al.*, Culling and cattle controls influence tuberculosis risk for badgers, *Proc Natl Acad Sci U S A* **103** (2006), pp. 14713–14717. View Record in Scopus | Cited By in Scopus (30)

13 King D. Bovine tuberculosis in cattle and badgers: a report by the Chief Scientific Adviser. 2007. Available at: http://www.defra.gov.uk/animalh/tb/pdf/badgersreport-king.pdf (accessed April 2008).

14 Bourne FJ, Donnelly CA, Cox DR, Gettinby G, McInerney JP, Morrison WI, et al. Response to “Tuberculosis in cattle and badgers: a report by the Chief Scientific Adviser”. 2007. Available at: http://www.defra.gov.uk/animalh/tb/isg/pdf/isg-responsetosirdking.pdf (accessed April 2008).

15 S.J. More, T.A. Clegg, G. McGrath, J.D. Collins, L.A. Corner and E. Gormley, Does reactive badger culling lead to an increase in tuberculosis in cattle?, *Vet Rec* **161** (2007), pp. 208–209. View Record in Scopus | Cited By in Scopus (8)

16 Environment Food and Rural Affairs Committee. Badgers and cattle TB: the final report of the Independent Scientific Group on Cattle TB. Fourth Report of Session 2007-8. Available at: http://www.publications.parliament.uk/pa/cm200708/cmselect/cmenvfru/130/130i.pdf (accessed April 2008).

17 National Farmers’ Union. NFU consultation response. 2006. Available at: http://www.nfuonline.com/documents/Policy Services/Animal and Plant health/PS06 057 Badger culling consultation FINAL v1.pdf (accessed April 2008).

18 RSPCA. RSPCA response to the public consultation. 2006. Available at: http://www.rspca.org.uk/servlet/Satellite?pagename=RSPCA/RSPCARedirect&pg=badgers&marker=1&articleId=1137587636944 (accessed April 2008).

19 The Mammal Society. A response to the public consultation. Controlling the spread of bovine tuberculosis in high incidence areas in England: badger culling. 2006. Available at: http://www.abdn.ac.uk/mammal/badgers_tb_consultation.shtml (accessed April 2008).

20 Defra. Controlling the spread of bovine tuberculosis in cattle in high incidence areas in England: badger culling. Defra, 2005. Available at: http://www.defra.gov.uk/animalh/tb/pdf/badger-consult.pdf (accessed April 2008).

21 Defra. Public consultation on controlling the spread of bovine tuberculosis in cattle in high incidence areas in England: badger culling – Summary of responses. Defra, 2006. Available at: http://www.defra.gov.uk/animalh/tb/pdf/summaryofresponses.pdf (accessed April 2008).

22 R. Woodroffe, F.J. Bourne, C.L. Cheeseman, D.R. Cox, C.A. Donnelly and G. Gettinby *et al.*, Welfare of badgers (*Meles meles*) subjected to culling: development and evaluation of a closed season, *Anim Welfare* **14** (2005), pp. 19–25. View Record in Scopus | Cited By in Scopus (12)

23 R. Woodroffe, F.J. Bourne, C.L. Cheeseman, D.R. Cox, C.A. Donnelly and G. Gettinby *et al.*, Welfare of badgers (*Meles meles*) subjected to culling: patterns of trap-related injury, *Anim Welfare* **14** (2005), pp. 11–17. View Record in Scopus | Cited By in Scopus (15)

24 Woodroffe R, Donnelly CA, Wei G, Bourne FJ, Cheeseman CL, Cox DR, et al. Patterns of trap-related injury recorded in the Randomised Badger Culling Trial—an update. Defra, 2007. Available at: http://www.defra.gov.uk/animalh/tb/isg/pdf/trapinjuries.pdf (accessed April 2008).

25 J.K. Kirkwood, Report of the independent auditor on the humaneness of the despatch procedures used in the Randomised Badger Culling Trial and MAFF's response. MAFF Publications, PB5325, MAFF, London, UK (2000).

26 R. Woodroffe, P. Gilks, W.T. Johnston, A.M. Le Fevre, D.R. Cox and C.A. Donnelly *et al.*, Effects of culling on badger abundance: implications for tuberculosis control, *J Zool* **274** (2008), pp. 28–37. View Record in Scopus | Cited By in Scopus (8)

27 R. Woodroffe and D.W. Macdonald, Costs of breeding status in the European badger, *Meles meles*, *J Zool* **235** (1995), pp. 237–245. View Record in Scopus | Cited By in Scopus (32)

28 R. Woodroffe and D.W. Macdonald, Helpers provide no detectable benefits in the European badger (*Meles meles*), *J Zool* **250** (2000), pp. 113–119. View Record in Scopus | Cited By in Scopus (40)

29 C.L. Cheeseman, P.J. Mallinson, J. Ryan and J.W. Wilesmith, Recolonisation by badgers in Gloucestershire. In: T.J. Hayden, Editor, *The badger*, Royal Irish Academy, Dublin, Ireland (1993), pp. 78–93.

Appendix A. Supplementary data

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