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Impacts of widespread badger culling on cattle tuberculosis: concluding analyses from a large-scale field trial

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Summary
Background: Bovine tuberculosis (TB) has re-emerged as a major problem for British cattle farmers. Failure to control the infection has been linked to transmission from European badgers; badger culling has therefore formed a component of British TB control policy since 1973.
Objectives and design: To investigate the impact of repeated widespread badger culling on cattle TB, the Randomised Badger Culling Trial compared TB incidence in cattle herds in and around ten culling areas (each 100 km^2) with those in and around ten matched unculled areas.
Results: Overall, cattle TB incidence was 23.2% lower (95% confidence interval (CI) 12.4—32.7% lower) inside culled areas, but 24.5% (95% CI 0.6% lower—56.0% higher) higher on land $\leq$2 km outside, relative to matched unculled areas. Inside the culling area boundary the beneficial effect of culling tended to increase with distance from the boundary ($p = 0.085$) and to increase on successive annual culls ($p = 0.064$). In adjoining areas, the detrimental effect tended to diminish on successive annual culls ($p = 0.17$). On the basis of such linear trends, the estimated net effect

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per annum for culling areas similar to those in the trial was detrimental between the first and second culls, but beneficial after the fourth and later culls, for the range of analyses performed.
Conclusions: Careful consideration is needed to determine in what settings systematic repeated culling might be reliably predicted to be beneficial, and in these cases whether the benefits of such culling warrant the costs involved.

Introduction

Bovine tuberculosis (TB) is a serious disease of cattle, which has re-emerged as a major problem for British cattle farmers in the last two decades.[1] From the 1950s onwards, routine testing of cattle combined with slaughter of affected animals, successfully eliminated the infection from much of Britain. However, infection remained in some areas, and this was linked to infection of local badger (*Meles meles*) populations with *Mycobacterium bovis*, the causative agent of the disease.[1] To try to reduce transmission of infection from badgers to cattle, badger culling formed a component of British TB control policy from 1973 until the start of the Randomised Badger Culling Trial (RBCT). Both the incidence and geographical extent of cattle TB have been increasing since the 1980s.[1]

The RBCT was launched in 1998 to evaluate the effectiveness of badger culling as a control strategy for cattle TB in Britain.[2] The RBCT involved 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 recruited as matched sets of three, known as 'triplets'. Results from the RBCT, published shortly after the suspension of reactive culling[3,4] and the completion of proactive culling,[5] showed that widespread proactive culling reduced cattle TB incidence inside the culled areas, but elevated incidence in neighboring unculled areas, apparently because culling induced changes in badger behavior, which increased the transmission of infection both between badgers, and from badgers to cattle.[6,7] Localized reactive culling likewise was associated with an overall detrimental effect,[3,4] apparently for similar ecological reasons.

If culling-induced changes to badger behavior and ecology do indeed influence TB dynamics, several predictions can be made about the impact of culling on TB risks for cattle. First, the benefits of proactive culling would be expected to increase as repeated culls are performed. This is because surveys for signs of badger activity indicate that badger density decreased with repeated proactive culling.[8]

A second prediction is that the beneficial effects of badger culling should vary with distance inside the culling area boundary. This is because the proportion of badgers captured close to the culling area boundary increased on successive culls (probably due to immigration from surrounding areas),[8] indicating that a more thorough removal was sustained deeper inside trial areas. Additionally, the initial prevalence of *M. bovis* infection in badgers was lower close to culling area boundaries than deeper inside, but on successive culls prevalence rose more markedly close to the boundaries.[7] If *M. bovis* prevalence in badgers reflects TB risk to cattle, these differences would be expected to influence the beneficial effects of culling.

A third prediction is that the effects of badger culling could be influenced by geographical barriers to badger movement. The published association between repeated proactive culling and increased *M. bovis* infection in badgers was observed only in trial areas where landscape conditions allowed badgers to immigrate into culled areas from neighboring land; no such effect was seen where coastline, major rivers or motorways formed a substantial proportion of trial area boundaries.[7] Hence, geographical barriers to badger movement might also affect the impact of culling on cattle TB.

A fourth and final prediction is that the beneficial effects of badger culling might be influenced by land access. Landholder consent was required before field staff could survey or cull badger populations. Every trial area contained land where consent was refused, and land for which no landholder could be identified. No traps were set on such land, although efforts were made to capture badgers residing in these areas by trapping around their boundaries. Nevertheless, the benefits of proactive culling observed on accessible land might be expected to be greater than those observed overall. Additionally, since cattle TB incidence was elevated on unculled land immediately outside culling areas, similar detrimental effects might be expected on land inside trial areas that was not accessible for culling.

All of these predictions have implications for the design of any future badger culling strategies. Here, we extend previous analyses[5] of the impacts of proactive culling using further data, and investigate whether such impacts varied with successive culls, herd location relative to trial area boundaries, permeability of trial area boundaries for badgers, and land accessibility for culling. We also explore the impact of land access on badger removal rates.

Materials and methods

Trial design and implementation

Thirty trial areas, each about 100 km^2, were recruited as ten matched triplets, located in areas of high cattle TB incidence (Figure 1). In most cases trial area boundaries followed property boundaries, but where possible, they followed geographic features likely to impede badger movement (coastline, rivers, large conurbations, motorways and dual carriageways). Boundary permeability was measured as the proportion of the perimeter not composed of such geographical barriers.[7] Neighboring trial areas were separated by buffer zones at least 3 km wide. All trial areas were surveyed for badger activity and then randomly allocated to treatments (except in one triplet where security concerns directed a specific allocation) such

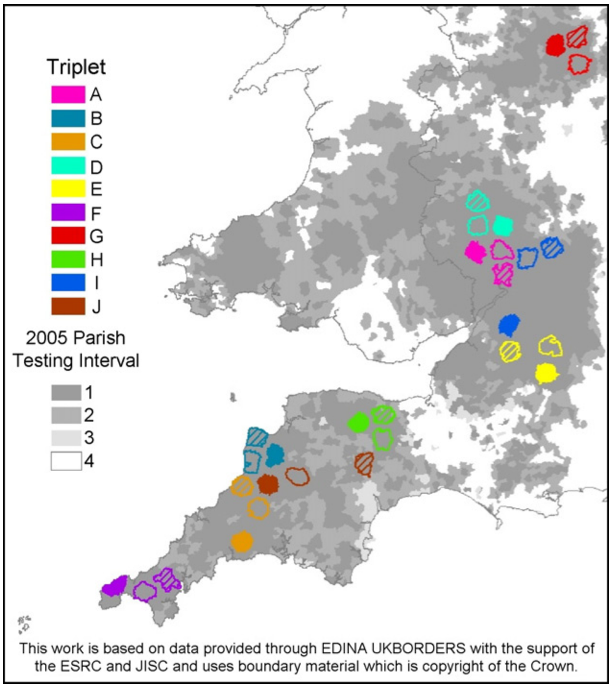

Figure 1 Locations of RBCT trial areas, denoting areas allocated to proactive culling (solid shading), reactive culling (hatched shading), and survey-only (open). Parish testing interval gives an indication of local cattle TB incidence. (Reproduced from the supplementary information to Donnelly CA, Woodroffe R, Cox DR, Bourne FJ, Cheeseman CL, Wei G, et al. Positive and negative effects of widespread badger culling on cattle tuberculosis. *Nature* 2006;**439**:843–6.).

that each treatment – proactive culling, reactive culling, or survey only (no culling) – was repeated ten times, once within each triplet.

Initial consent was sought from landholders before areas were surveyed for badger activity and culling treatments allocated. Landholders consented to surveying and culling ('culling' land), surveying but not culling ('survey' land), or refused all access ('refusal' land). Additionally, each trial area contained land for which no landholder could be identified ('unsigned' land). Landholders could change consent status at any time. Following treatment allocation, initial culls were conducted on all land in the proactive areas for which consent was given. Culling treatment area boundaries were defined (beyond trial area boundaries where necessary) using field survey data to ensure that all badgers likely to use land inside the trial areas were targeted. Badgers were captured in cage traps placed primarily at setts. Trapping was suspended in February–April each year to avoid killing mothers with dependent cubs still confined to the sett.[9,10] Few badgers sustained trap-related injuries,[11,12] and dispatch (by gunshot) was deemed 'humane' by independent audit.[13–17] Initial culls for each proactive trial area were completed between December 1998 and December 2002, and 'follow-up' culls were repeated approximately annually (with longer delays incurred due to a nationwide epidemic of foot-and-mouth disease in 2001).[7]

As soon as the initial proactive cull was complete, data were collected on cattle TB incidence in and around trial areas, using established veterinary surveillance. Surveillance distinguished 'confirmed breakdowns' (incidents in which postmortem examination of slaughtered cattle led to detection of TB lesions or culture of *M. bovis*) from 'unconfirmed breakdowns' (incidents in which one or more cattle reacted to the tuberculin test but infection was not confirmed at postmortem or by culture). Here our primary analyses were based on the incidence of confirmed breakdowns; analyses of all breakdowns (confirmed and unconfirmed), and unconfirmed breakdowns only, are presented and discussed in supplementary material.

Analyses of the effect of land accessibility used the earliest available data on the consent status of each land parcel, since interpretation of consent-stratified analyses of cattle TB incidence would be invalid if changes in consent depended on culling-induced changes in the local risk of cattle TB (although no evidence of such dependence has been found, see supplementary material for details). The proportion of inaccessible ('survey', 'refusal' or 'unsigned') land within proactive treatment areas varied from 15% to 50% (30% overall). In total, 73% of inaccessible land was within 200 m of accessible ('culling') land (see supplementary material).

Effects of proactive culling on TB incidence in cattle

Statistical analysis methods were similar to those previously published.[5] Log-linear Poisson regression was used to compare the numbers of breakdowns recorded in trial areas subjected to the proactive and survey-only treatments, adjusting for triplet, the log of the number of baseline herds at risk, and the log of the number of confirmed breakdowns recorded either one or three years prior to RBCT culling. To minimize bias in the covariates, 0.5 was added to the numbers of baseline herds and historic confirmed breakdowns before the logs were taken.[18] Other measures of the at-risk population were explored in supplementary material. As in previous analyses,[5] 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.

Cattle herd locations were taken from two alternative databases, the national animal health information system VetNet, and a separate database set up specifically for the RBCT. Analyses performed using these two databases are presented separately. These databases were used to identify herds inside, and up to 2 km outside, trial area boundaries. The VetNet database provided more complete data on herds outside trial areas, because the RBCT database did not include all farms on neighboring land. Herds within 2 km of more than one trial area boundary (whether proactive, reactive or survey-only) were omitted from analyses.

Primary analyses covered the period from the initial proactive cull in each triplet, to a date one year after culling had ceased in that triplet, when another cull would have occurred had proactive culling continued. This time period – which totalled 55.8 triplet-years – also offered an opportunity for annual herd testing to detect any breakdowns that occurred during the culling period. Estimates obtained in the current analyses may differ slightly from previously published estimates for the same time periods due to an improvement in the linking of herds to their breakdowns in the surveillance database. Additional estimates of the effect of proactive culling were obtained from stratified data for accessible and inaccessible land, for different time periods, and for different distances from the trial area boundary. Tests for linear trends (on the log scale) with the number of repeat culls and distance from the trial area boundary were performed using weighted least squares. The effects of boundary permeability were investigated by adding a main effect of permeability and a treatment × permeability interaction term to the log-linear models, tests of the latter being of interest. Several other factors (e.g., measures of initial badger density) were hypothesized to influence the impact of culling; these are detailed in supplementary material. The findings based on spatial—temporal variation within trial areas are independent of the randomization used in the primary comparisons of the trial.

Effects of land access on proactive badger removal

Badgers were trapped only on land inside treatment areas where 'cull' consent had been given. However, efforts were made to capture badgers resident on inaccessible land by placing traps on nearby accessible land. To assess the effectiveness of these efforts we analyzed capture rates within 200 m of inaccessible land within trial areas (the 200 m distance being dictated by the precision of recording capture locations on 1:10 000 maps and the need to place traps at locations such as badger setts or paths). To avoid including badgers immigrating from outside the proactive treatment area, we excluded land <200 m inside the treatment area boundary. Parallel analyses investigated whether findings were influenced by badger preference for any property boundary (irrespective of consent status) but gave similar results (see supplementary material).

The badger removal rate on accessible land (less the 200 m zones around inaccessible land) was compared with that in the 200 m zones, and with that in the inaccessible land and 200 m zones combined. Numbers of badgers caught were compared using log-linear models, adjusting for triplet and log-transformed land area (km^2). We also investigated interactions between badger capture locations and cull type (initial vs. follow-up).

Results

During the entire study period there were 472 confirmed breakdowns among herds identified by VetNet as being inside the proactive trial areas, and 362 confirmed breakdowns on land up to 2 km outside. Inside proactive trial areas, 245 herds had a single confirmed breakdown, 74 herds had two confirmed breakdowns, and 25 herds had more than two (3.16 on average). On the land up to 2 km outside proactive trial areas, 191 herds had a single confirmed breakdown, 58 herds had two confirmed breakdowns, and 17 herds had more than two (3.24 on average).

Overall effects of proactive culling on TB incidence in cattle

The primary analysis revealed that the overall incidence of confirmed TB breakdowns in cattle was 23.2% (95% CI 12.4—32.7%) lower inside proactively culled trial areas than inside unculled survey-only areas ($p < 0.001$). This effect was consistent across all ten proactive/survey-only pairs (the test for overdispersion was not significant, $p = 0.87$). As in previous

Table 1 Estimated effects of proactive culling on the incidence of confirmed cattle TB breakdowns. Analyses adjusted for triplet, baseline herds, and historic TB incidence (over three years)

	Proactive effect			Overdispersion	
	Estimate	95% CI	*p*-Value	Factor	*p*-Value
Inside trial areas					
Using VetNet location data					
From initial cull (cull 1)	−23.2%	(−32.7%, −12.4%)	<0.001	0.67	0.87
From first follow-up cull (cull 2)	−26.6%	(−36.8%, −14.8%)	<0.001	0.93	0.53
Between initial and follow-up	−7.2%	(−31.3%, 25.4%)	0.63	1.05	0.36
Using RBCT location data					
From initial cull (cull 1)	−17.4%	(−27.2%, −6.2%)	0.003	0.79	0.74
From first follow-up cull (cull 2)	−21.0%	(−31.6%, −8.8%)	0.001	0.86	0.64
Between initial and follow-up	1.1%	(−26.4%, 39.0%)	0.94	1.15	0.23
Up to 2 km outside trial areas					
Using VetNet location data					
From initial cull (cull 1)	24.5%	(−0.6%, 56.0%)	0.057	1.26	0.13
From first follow-up cull (cull 2)	19.6%	(−10.3%, 59.5%)	0.22	1.41	0.052
Between initial and follow-up	46.8%	(−0.4%, 116.4%)	0.052	0.95	0.50
Using RBCT location data					
From initial cull (cull 1)	35.3%	(5.8%, 73.0%)	0.016	1.00	0.44
From first follow-up cull (cull 2)	24.9%	(−7.2%, 67.9%)	0.14	1.09	0.34
Between initial and follow-up	95.4%	(10.5%, 245.5%)	0.021	0.82	0.69

RBCT, Randomised Badger Culling Trial.

analyses,[5] this effect was somewhat stronger when measured from the first follow-up cull (cull 2), rather than the initial cull (cull 1; Table 1). Similar results were achieved if the RBCT database (rather than the VetNet database) was used to identify cattle herds inside trial areas (Table 1), and if analyses adjusted for historic incidence in the previous year (rather than the previous three years; details in supplementary material). Furthermore, findings were robust to the use of different measures of the size of the cattle population at risk (see supplementary material).

On land up to 2 km outside proactive trial areas, overall cattle TB incidence was 24.5% higher (95% CI 0.6% lower—56.0% higher) than that on land neighboring survey-only areas ($p = 0.057$). Once again, the effect was consistent across all ten proactive/survey-only pairs (the test for overdispersion was not significant, $p = 0.13$). Similar patterns were detected using herd locations from the RBCT database, and adjusting for one year's historic incidence (see supplementary material). Interestingly, this detrimental effect of culling was most marked between the initial and first follow-up cull; weaker detrimental effects were detected after the first follow-up cull (Table 1).

These results can be used to estimate the number of confirmed breakdowns prevented, and induced, by proactive culling. If we assume that a 100-km^2 circular area were culled, then just under 83.5 km^2 of land is within 2 km of the culling area boundary. If the herd density were 1.25 per km^2 (roughly that seen in trial areas), then there will be 125 herds in the culling area and 104 in the neighboring area. If the underlying incidence rate throughout ten such areas were 8 confirmed breakdowns per 100 herds per year, then these results are equivalent to the saving of an estimated 116 fewer confirmed breakdowns (10 areas × 125 herds × 8 confirmed breakdowns/100 herds per year × 5 years × 0.232) over 5 years in the culling areas and an estimated 102 additional breakdowns (10 areas × 104 herds × 8 confirmed breakdowns/100 herds per year × 5 years × 0.245) over 5 years in the neighboring areas due to proactive culling, for a net benefit of 14 fewer breakdowns over 5 years across the ten 183.5 km^2 combined areas. If the underlying incidence rate were lower in the neighboring area than in the culling area, then this net benefit would be greater. However, unless this underlying rate is considerably lower than that in the culling area, the 95% prediction interval for the net benefit will include zero.

Effect of repeated proactive culling on cattle TB incidence

When the data were stratified based on the intervals between successive culls (initial to second, second to third, third to fourth, and after fourth), the beneficial effect of proactive culling inside trial areas appeared to increase with repeated culling (Figure 2A). The linear trend (on the log scale) suggested an 11.2% increase in the beneficial proactive effect with each cull ($p = 0.064$). Correspondingly, the detrimental effect of proactive culling in the neighboring area appeared to diminish with each cull (Figure 2A), with the linear trend suggesting a 7.3% decrease in the detrimental proactive effect with each cull ($p = 0.17$). Based on the estimates from the models with linear trends, the estimated net effect per annum appeared detrimental between the first and second culls, but beneficial after the third and later culls. Similar non-significant trends were found adjusting for one year's historic incidence and using herd locations from the RBCT database adjusting for three years' historic incidence (see supplementary material). For the range of analyses performed, the estimated net effect per annum was detrimental between the first and second culls, but beneficial after the fourth and later culls.

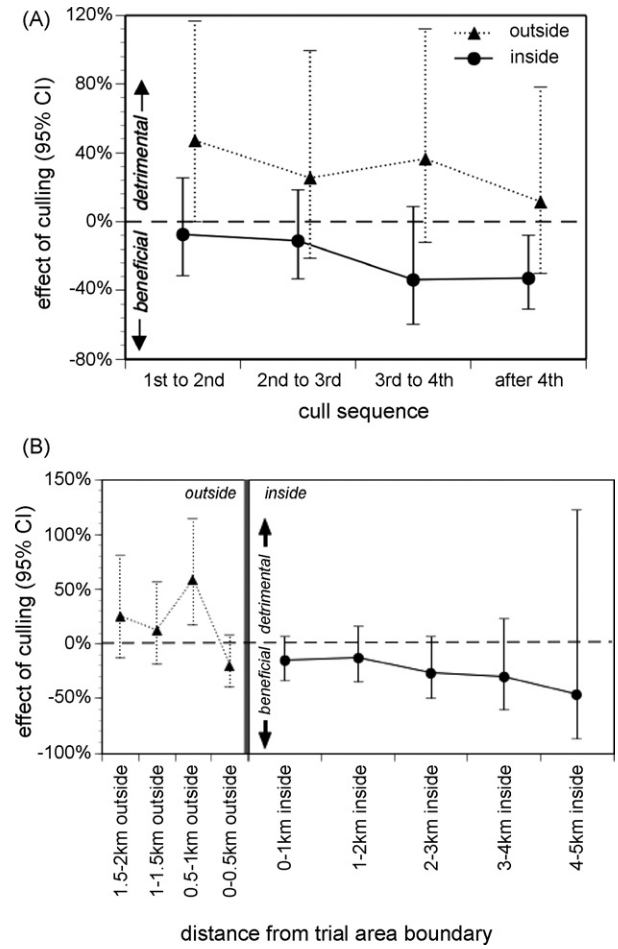

Figure 2 (A) Variation in the effect of proactive culling by the number of repeat culls. (B) Variation in the effect of proactive culling at different distances from the trial area boundary. These analyses used cattle herd locations from the VetNet database and adjusted for historic cattle TB incidence (over three years). Error bars denote 95% confidence intervals.

Dependence of the effects of proactive culling on proximity to the boundary

The beneficial effect of proactive culling appeared to increase at greater distances inside the trial area boundary (Figure 2B, $p = 0.085$). Detrimental effects of culling were observed for herds 0.5—2 km outside the trial area boundary, while those within 0.5 km of the trial area boundary appeared to experience a benefit (Figure 2B). This latter effect was unsurprising, because badger culling extended beyond the boundaries of the trial areas to target social groups judged, on the basis of field signs, to occupy home ranges falling partially inside the trial areas.

There was no evidence that this dependence in the effect of culling on proximity to the boundary changed in response to repeated culling (see supplementary material).

Effects of boundary permeability

In badgers, the permeability of culling area boundaries was previously shown to have a marked effect on how *M. bovis* prevalence changed on successive culls.[6] However, the overall effect of culling on cattle TB was not significantly modified by boundary permeability either inside trial areas ($p = 0.73$) or on neighboring lands ($p = 0.69$). As only two proactive trial areas had more than 20% of their boundaries relatively impermeable to badgers, it was not possible to stratify analyses of time trends by boundary permeability.

Effects of land access on the impact of proactive culling on cattle TB

Comparing TB incidence in herds on accessible proactive land with entire survey-only areas indicated effects of culling comparable in magnitude and precision with those observed on proactive land as a whole (Table 2). Effects of culling on inaccessible proactive land were estimated less precisely and were thus less consistent between models using the VetNet and RBCT databases. As the estimates from inaccessible land were of limited precision, it was unsurprising that comparisons between effect estimates based on accessible and inaccessible land showed no significant differences ($p = 0.36$ using herd locations from the VetNet database, Table 2).

Effects of land access on badger removal rates

Data on capture rates suggest that substantial numbers of badgers were removed from inaccessible land by trapping in the surrounding 200 m zones. If badger density was uniform across trial areas and no badgers were taken from inaccessible land then, based on the relative area of accessible land, inaccessible land, and 200 m zones, 44% fewer captures would be expected per km^2 in 200 m zones plus inaccessible land than on the remaining accessible land. In fact, on initial culls, only 28% fewer badgers were taken from each km^2 of 200 m zones plus inaccessible land, with the 95% CI (8%–43% fewer, $p = 0.007$ for the hypothesis of no difference between capture rates) indicating a removal rate significantly greater than expected (44% fewer, $p = 0.033$). This effect differed (interaction $p = 0.014$) between initial and follow-up culls; on follow-ups there was no difference in removal rate between land types with different accessibility (3% fewer on inaccessible land plus 200 m zones; 95% CI 17% more–20% fewer; $p = 0.74$).

On initial culls, there was no difference between badger capture rates in the 200 m zones and on remaining accessible land (2% more per km^2 in 200 m zones; 95% CI 18% fewer–26% more, $p = 0.88$). On follow-up culls more badgers may have been culled per km^2 in the 200 m zones (18% more, 95% CI 1% fewer–39% more, $p = 0.060$). However, the difference between removal rates in 200 m zones and the remaining accessible land did not vary significantly between initial and follow-up culls ($p = 0.29$).

Discussion

The results presented here extend those published previously, and provide further evidence that the impact of badger culling on cattle TB incidence depends critically upon the geographic extent and temporal pattern of culling. This information will be very important in deciding whether badger culling should contribute to future strategies to control cattle TB.

The inclusion of additional data confirmed our previous finding — that proactive culling has the capacity to both decrease and increase the incidence of cattle TB[5] — but improved the precision of the estimates. As predicted, the beneficial effects of proactive culling tended to become more marked on successive culls; this is consistent with the finding that badger density inside proactive areas declined over the same period.[8] By contrast, the detrimental effects of culling detected on neighboring land were initially

Table 2 Estimated effect of proactive culling on the incidence of confirmed TB breakdowns. Analyses adjusted for triplet, baseline herds, and historic TB incidence (over three years). All herds in proactive trial areas are compared with all those in survey-only trial areas, and then the comparison is stratified by consent status of land

Source of herd location data	Consent status	Baseline herds (proactive/survey-only)	Proactive effect			Overdispersion		*p*-Value for difference between accessible and inaccessible[a]
			Estimate	95% CI	*p*-Value	Factor	*p*-Value	
VetNet	All proactive land[b]	1221/1276	−23.2%	(−32.7%, −12.4%)	<0.001	0.67	0.87	–
	Accessible	812/817	−15.4%	(−29.9%, 2.0%)	0.080	1.33	0.009	0.36
	Inaccessible	409/459	−28.7%	(−48.6%, −1.0%)	0.044			
RBCT	All proactive land[b]	1009/1127	−17.4%	(−27.2%, −6.2%)	0.003	0.79	0.74	–
	Accessible	834/873	−15.5%	(−28.1%, −0.6%)	0.042	1.25	0.034	0.82
	Inaccessible	175/254	−10.6%	(−42.4%, 38.6%)	0.615			

RBCT, Randomised Badger Culling Trial.
[a] 95% CI for the difference in the effect of proactive badger culling between herds on accessible and inaccessible land: VetNet, −17.8%, 71.0%; RBCT, −41.0%, 51.7%.
[b] Estimates comparable to those presented in Donnelly et al.,[5] but using incidence data up to a date one year after culling had ceased in that triplet.

substantial, but may have become less strong on later culls. As a result, the estimated net impact of proactive culling observed in the RBCT transitioned from being detrimental between the initial and second culls, to being beneficial after the fourth and later culls.

The balance of benefit and detriment would clearly be affected by the size of the area culled (and hence the relative proportions of land falling inside, and immediately outside, the culling area). Likewise, our analyses illustrate the sensitivity of the outcome to the baseline incidence of cattle TB inside and outside the culling areas. In the RBCT, trial areas were centered on areas of high cattle TB risk, so baseline incidence was higher in the culling (and matched survey-only) areas than on neighboring land. Had trial areas been located such that background incidence was equivalent inside and immediately outside the areas culled (but with the same underlying proportions of breakdowns due to badgers inside and immediately outside the areas as in the trial), the estimated absolute number of breakdowns induced would have been greater, reducing the overall benefits.

Our findings confirm that infectious contact between badgers and cattle is related to badger density in a manner that is strongly non-linear. At the comparatively high population densities that were observed inside survey-only areas, and would have occurred in proactive areas prior to culling, badgers occupy small territories and *M. bovis* infection is highly clustered.[6,19–22] This territorial organization presumably limits, to some extent, the risk of cattle herds encountering infectious badgers. Substantially lowering density by repeated proactive culling disrupted territorial organization, expanded movement patterns, and elevated *M. bovis* prevalence in badgers,[6,7] but presumably reduced badger—cattle contact to such an extent that incidence was reduced in cattle. This reduction was not achieved immediately, probably because more thorough badger removal was sustained on later culls.[8]

A different pattern occurred on unculled land immediately outside proactive culling areas. Badger densities were reduced only slightly, but spatial organization was disrupted and movement patterns were expanded, as in culled areas.[6] Because expanded ranging was observed in the absence of a major reduction in density, the risks of infectious contact between badgers, and between badgers and cattle, were probably elevated, rather than reduced, by culling. The reduction in density was smallest immediately after initial culls[8] and this pattern, together with field evidence that badgers alter their movement patters rapidly in response to disturbance,[23–25] may explain why the detrimental effect on cattle TB was particularly marked at this time (Figure 2A).

We speculate that the reduced detrimental effect observed in neighboring areas on later culls (Figure 2A) may have reflected changes in the structure of badger populations prompted by repeated culling. Although social disruption has been shown to alter badger movement patterns on a timescale of days or weeks,[23–25] depletion of the badger population on land neighboring trial areas may have taken several years. This is because culling is likely to have prompted not only expansion of badgers' daily ranges (as measured in the RBCT[6]) but also increased dispersal (that is, a permanent shift of an individual's home range from one location to another; this occurs more commonly in badger populations living at low population densities[25]). Dispersal can take several months to complete[26] and, in young animals at least, is likely to be seasonal; hence dispersal into culled areas may continue to occur in the months or years after completion of each cull. However, since most dispersal occurs over short distances (1—2 territories in undisturbed populations[25,27]), repeated culling is likely to have eventually depleted the pool of dispersers and allowed a quasi-stable spatial organization to re-emerge. This might explain the reduced detrimental effect apparently recorded on neighboring lands on later proactive culls. Unfortunately, this hypothesis cannot be tested because monitoring of badger activity across successive culls was confined to the trial areas themselves, and not conducted outside. However, if this interpretation were correct, it would suggest that an equivalent reduction in the detrimental effect would probably not be achieved by conducting the same number of culls over a much shorter period. There was no evidence that the distribution of detrimental effects, relative to the culling area boundary, changed consistently over time (see supplementary material).

As expected, the beneficial effect of badger culling on cattle TB appeared more marked at greater distances inside the trial area boundary (Figure 2B). This was predicted both because badger removal was more thorough deeper inside trial areas,[8] and also because the prevalence of *M. bovis* infection in badgers was higher on such land, particularly on initial culls.[7] However, as there was no evidence that the dependence of the beneficial effects on proximity to the trial area boundary changed over successive culls (see supplementary material), this pattern is most likely to reflect the degree to which badger population densities were reduced at greater distances from the culling area boundary.

The effect of culling on *M. bovis* prevalence in badgers was influenced by the permeability of trial area boundaries.[7] However, no such effect on the incidence of cattle TB was detected, either inside or outside trial area boundaries. This may be because of limited statistical power: the RBCTwas not designed to test this hypothesis[2] and the variation among trial areas in boundary permeability was not great.[7] Thus, currently available data shed no direct light on whether a proactive culling policy would be more beneficial — or less detrimental — if conducted in more geographically isolated areas.

The prevalence of *M. bovis* infection in badgers was also elevated following a nationwide epidemic of foot-and-mouth disease, during which routine cattle TB testing was suspended.[7] However, there was no evidence that this influenced the beneficial or detrimental effects of badger culling on cattle TB (details in supplementary material).

There was no evidence that lack of consent to cull (at the level and configuration observed in the RBCT) undermined the beneficial effects of badger culling: the incidence of cattle TB on accessible land was comparable with that observed overall and not significantly different from that on inaccessible land. This contrasts with the situation observed immediately outside trial areas, where herds on unculled land experienced elevated TB incidence. This difference probably reflects the substantial ecological differences between the two types of unculled land. Inaccessible areas were mostly small relative to badger home range size: 95% of the inaccessible land fell within 500 m of culling areas, comparable with the median ranging distances of badgers in proactive areas (300–700 m).[6] As most inaccessible land was completely surrounded by culled land, there were opportunities to capture badgers resident on inaccessible land in traps placed on nearby accessible land. In contrast, survey data indicate that the unculled land surrounding proactive treatment areas contained large, contiguous and mostly intact badger populations, which could provide a source of colonists to re-occupy land cleared by culling. Hence, the dynamics of badger–badger and badger–cattle interactions would be expected to differ in the two types of unculled land.

These findings have important implications for decisions about whether badger culling should contribute to future strategies to control cattle TB.[28] Results confirm that badger culling is only likely to be beneficial if conducted systematically over large areas, and sustained over several years. Previous analyses have suggested that culling conducted in small, localized areas has overall detrimental effects,[3,4] and analyses presented here indicate that the detrimental effects of widespread culling outweigh the benefits if culling is not sustained. Our results also suggest that careful deployment of traps around inaccessible land contributed to the beneficial effects of culling reported here. Detailed consideration would be needed to determine whether this level of effort would be feasible in the long term, and whether the level of disease control achieved would be sufficient to warrant the costs involved.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ijid.2007.04.001.

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