

Effects of culling on badger abundance: implications for tuberculosis control

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Abstract

Culling is often considered as a tool for controlling wildlife diseases that can also infect people or livestock. Culling European badgers *Meles meles* can cause both positive and negative effects on the incidence of bovine tuberculosis (TB) in cattle. One factor likely to influence the outcome of different badger culling strategies for cattle TB is the reduction in badger population density achieved. However, this reduction is difficult to measure because badgers, being nocturnal and fossorial, are difficult to count. Here, we use indices of badger abundance to measure the population impacts of two culling strategies tested in Britain. The densities of badger setts and latrines recorded before culling were correlated with the densities of badgers captured on initial culls, suggesting that both were indices of actual badger abundance. Widespread 'proactive' culling was associated with a 73% reduction in the density of badger latrines, a 69% reduction in the density of active burrows and a 73% reduction in the density of road killed badgers. This population reduction was achieved by a coordinated effort entailing widespread and repeated trapping over several years. However, this strategy caused only modest reductions in cattle TB incidence in culled areas and elevated incidence in neighbouring uncultured areas. Localized 'reactive' culling caused a 26% reduction in latrine density, a 32% reduction in active burrow density and a 10% reduction in the density of road killed badgers, but apparently increased the incidence of cattle TB. These results indicate that the relationship between badger population reduction and TB transmission to cattle is strongly non linear, probably because culling prompts changes in badger behaviour that influence transmission rates. These findings raise serious questions about the capacity of badger culling to contribute to the control of cattle TB in Britain.

Introduction

Most models of infectious disease dynamics assume that contact rates between host organisms, and therefore transmission rates, decline as host population densities are reduced; the simplest models assume that this relationship is linear (Barlow, 1996). Likewise, where a pathogen can infect more than one host species, reducing the density of one host is expected to lower the interspecific transmission rate. Because host population reduction is expected to have these twin effects, culling is often considered as a means of controlling wildlife diseases that can also infect people or livestock (e.g. Ballantyne & O'Donoghue, 1954; Dobson & Meagher, 1996).

In the British Isles, European badgers *Meles meles* are implicated in spreading *Mycobacterium bovis* (the causative

agent of bovine tuberculosis, TB) to cattle. Badger culling has therefore formed a component of TB control policy for many years (Krebs *et al.*, 1997).

Recent field trials investigating the impacts of badger culling on TB dynamics suggest that the relationship between host density and disease transmission is far from linear. Different culling strategies have been associated with both reductions and increases in the prevalence of *M. bovis* infection in badgers (Griffin *et al.*, 2003; Woodroffe *et al.*, 2006b) and the incidence of TB in cattle (Donnelly *et al.*, 2003, 2006; Griffin *et al.*, 2005). The degree of badger population reduction achieved by culling is probably one factor contributing to this variation.

Assessment of the impact of culling on badger density is impeded by badgers' secretive nocturnal behaviour. Several

studies have demonstrated correlations between badger abundance and the densities of field signs such as setts (badger dens) and latrines (sites badgers visit regularly for scent marking), although predictive power varies between methods, sites and seasons (Tuytens *et al.*, 2001; Wilson *et al.*, 2003a; Sadler *et al.*, 2004).

Here, we use field data to assess the impacts of culling on badger populations in Britain's Randomized Badger Culling Trial (RBCT); we also describe the capture effort entailed in achieving such impacts. These data can be used to inform the design of future TB control strategies.

Methods

Overall study design

Data collection focused on 30 areas, each measuring *c.* 100 km² and located in regions of high TB risk to cattle (Woodroffe *et al.*, 2006b). These 30 areas were grouped into 10 'triplets' denoted A–J. Within each triplet, all three areas were simultaneously surveyed for signs of badger activity, and then randomly allocated to three treatments: wide spread 'proactive culling' (which aimed to maintain badger densities at low levels by culling across entire trial areas approximately annually); localized 'reactive culling' (which entailed one off small scale badger culling in response to specific TB outbreaks in cattle); and 'no culling' (an experimental control).

Triples were recruited sequentially. Initial proactive culls were conducted between 1998 and 2002. The reactive treatment was suspended in November 2003; hence, no reactive culling was conducted in Triplet J (Donnelly *et al.*, 2003). Proactive culling was completed in October 2005. Cull dates are given in Supplementary Material.

Badger trapping operations

Badgers were captured in cage traps baited with peanuts. All trapping was conducted during May–January to avoid catching lactating females with dependent cubs still confined to setts (Woodroffe *et al.*, 2005a). In proactive areas, trapping occurred across all properties to which landholders granted access. Reactive culling operations were restricted to the home ranges of badger social groups judged, from field surveys, to include land occupied by cattle herds that had experienced recent TB incidents.

Trap deployment at each capture site (usually a sett) was determined by the level of badger activity detected at the time, with the number of traps set intended to exceed the number of badgers that experienced field staff expected to capture. Traps were set after a 1–2 week prebaiting period. Standard operating procedures prescribed that initial proactive culling operations be conducted over 11 consecutive nights. Both 'follow up' proactive culls and reactive culls were conducted over eight nights. Captured badgers were dispatched by gunshot; independent audit deemed dispatch 'humane' (Kirkwood, 2000) and most badgers received no detectable injuries from confinement in the trap (Woodroffe

et al., 2005b). Captured animals other than badgers were released, or dispatched humanely if deemed too badly injured for release. Evidence of destruction, removal or interference with traps was recorded, as was evidence (e.g. vegetation pulled into trap) that traps had contained badgers subsequently released by protestors.

Measures of trapping effort, capture rate and interference were derived from Defra records. Data on trap deployment, captures and trap interference were available for each day and each sett on 44 proactive and 62 reactive culling operations; summary data were available for seven additional proactive operations (detailed in Supplementary Material). Capture rate was calculated as the number of badgers caught, divided by the number of traps available (i.e. not occupied by other species or subjected to interference) on a particular night.

Surveys of badger activity

Initial pre cull surveys of badger activity (denoted 'Survey One' in figures and tables) were conducted across all trial areas before treatments were allocated, on all properties to which landholders granted access (including areas where permission was given for surveying but not culling). Survey teams used 1:10 000 maps to record all badger setts and latrines encountered, estimating locations on a 100 m grid. At each sett, observers recorded the numbers of active holes (those showing evidence of repeated recent use, often with fresh digging or tracks), and inactive holes (without evidence of recent use, often blocked by cobwebs, accumulated leaves or other debris), as well as latrines, fresh digging and bedding. Setts were classified as 'main' or 'other' on the basis of their size, activity and location in relation to other nearby setts (Thornton, 1988); however, independent audit found that field staff appeared hesitant to identify 'main' setts (Cresswell, 2001) and so the numbers are probably underestimated. A small number of setts recorded before culling, but after treatment allocation, were excluded because survey effort was not consistent across trial areas once field staff were preparing for proactive culling. Latrine data could not be censored in the same way because mapping dates of individual latrines were not recorded.

Subsequent post cull 'follow up' surveys of badger activity were conducted on all accessible land (including land accessible for surveying but not culling) in sample areas, each covering 5% of a trial area. These surveys were conducted without reference to earlier maps, to ensure consistent data collection protocols across successive surveys. Each survey covered four or six sample areas, together comprising 20 or 30% of a trial area. There was some overlap in the sample areas chosen for inclusion in successive surveys. Follow up surveys were conducted *c.* 2 years after completion of each initial cull, and at least every 2 years thereafter; survey dates are given in Supplementary Material. For illustrative purposes, results are quoted for the fourth survey because this was the latest to be conducted in all 10 triplets.

Bait marking

More intensive surveys of badger activity were conducted in a subset of triplets in 2004–2005. These surveys used colour marked bait to delineate badger home ranges (Delahay *et al.*, 2000), and are described in detail in Woodroffe *et al.* (2006a). Study areas of *c.* 16 km² were located inside the reactive and no culling areas of Triplets B, D, G and H. Study areas of about 24 km² spanned the boundaries of proactive culling areas in B, C, D, G and H, allowing comparison of badger activity in *c.* 16 km² of culled land with that on adjoining land. We used the number of colour marked faecal deposits (bait returns) recorded per km² to indicate local badger activity. The uncultured portion of the proactive study area in Triplet G was small in comparison with other study areas (containing only one badger home range, Woodroffe *et al.*, 2006a), and the results from this area are therefore excluded.

Road traffic accident survey

The relative badger abundance was also estimated using a survey of badgers killed in road traffic accidents, conducted primarily to investigate regional patterns of *M. bovis* infection (Bourne *et al.*, 1998). This survey was conducted during 2002–2005 in seven counties, and covered all trial areas of Triplets A, B, C, D, F and J.

The numbers of carcasses retrieved annually were compared across treatments; proactive areas were also compared with a surrounding zone 5 km wide in which no culling was conducted. These analyses excluded data from Triplets D and J in 2002, because these areas only received their initial proactive culls in late 2002, while the majority of badger road kills occur in spring (Davies, Roper & Sheperdson, 1987).

Statistical analyses

Data were analysed using Poisson regression and unbalanced ANOVA. All statistical models include triplet as a covariate. Several analyses investigated temporal trends in badger activity (e.g. changes in latrine density on successive surveys) under different culling treatments. Data from the reactive treatment were excluded from these analyses because this treatment was suspended part way through the study; however, descriptive data from reactive areas are presented. Average values quoted for reactive areas exclude Triplet J because no reactive culling was conducted there. All time periods used in analyses (e.g. days since the start of a culling operation) were represented as categorical variables.

Where appropriate, analyses adjusted for seasonal variation in badger activity. Seasons were defined such that February–April was considered ‘spring’, May–July was ‘summer’, August–October was ‘autumn’ and November–January was ‘winter’.

Poisson regression analysis of the numbers of badgers captured in proactive areas considered two regions of each

trial area: an ‘outer’ (≤ 1 km inside) and an ‘inner’ (> 1 km inside) region. This analysis adjusted for the area of land accessible for culling in each region, as well as the numbers of traps deployed at setts. The locations of traps deployed away from setts were not recorded but the overall proportion of badgers caught away from setts in the inner region (18.4%) was similar to that in the outer region (21.3%), suggesting that trap deployment away from setts did not differ systematically between regions.

We assessed the utility of field signs as indices of actual badger density by comparing the numbers of badgers captured on initial culls within 2×2 km grid squares with the densities of setts and latrines recorded on pre-cull surveys in the same squares. Poisson regressions, adjusting for triplet and the total area of the square falling inside the culling area, were used to compare field sign densities (measured as numbers per km² available for surveying) with the numbers of adults captured. The results are reported for squares with $\geq 95\%$ (3.8 km²) inside the culling area, but the results were very similar when all squares were included, and when the total number of badgers (adults and cubs) was the outcome variable.

Further analyses explored the effects of culling on the persistence of particular setts between successive surveys; these are presented in Supplementary Material.

Results

Trapping effort

Proactive culling involved an estimated 160 893 trap nights conducted over 51 operations, with an average of 298.5 traps deployed per night on each operation (Table 1). Average proactive capture effort was 40 trap nights km⁻² year⁻¹ over periods of 4–7 years. The 62 reactive culling operations for which data were available comprised a total of 21 109 trap nights, with an average of 42.6 traps deployed per night on each operation.

As intended, the numbers of traps deployed at each sett exceeded the numbers of badgers caught in the majority of cases: on an average trap night, the proportion of setts where all available traps were occupied by badgers was 2.4% in proactive areas and 2.7% in reactive areas. This proportion declined rapidly through the course of an operation, from 9% (proactive) and 14% (reactive) on the first night to 1% (both proactive and reactive) by the third night.

Non target species (e.g. pheasants *Phasianus colchicus* and grey squirrels *Sciurus carolinensis*) were caught on about 1% of trap nights in both proactive (Table 1) and reactive (Table 2) areas.

Interference with trapping operations was recorded on all 51 proactive culling operations and on 30 of 62 reactive culling operations for which data were available. Overall, such interference affected 8.1% of trap nights on proactive culling operations (Table 1), and 4.6% of trap nights on reactive culling operations (Table 2).

Occasionally, interference and capture of non target species together meant that no traps were available to

Table 1 Capture rate, and interference with trapping, on culling operations conducted in proactive areas, summarized by triplet

Triplet	Number of operations	Area accessible to cull (km ²)	Total trap nights ^a	Number (%) animals caught		Number (%) trap nights disrupted	
				Badgers ^b	Other species ^c	Badgers released	Other interference
A	5	82.2	10 751	362 (3.9%)	176 (1.6%)	12 (0.1%)	1232 (11.5%)
B	7	88.2	26 806	787 (3.1%)	181 (0.7%)	28 (0.1%)	1276 (4.8%)
C	6	98.2	22 111	964 (4.7%)	120 (0.5%)	36 (0.2%)	1637 (7.4%)
D	4	75.9	13 841	1051 (8.4%)	160 (1.2%)	12 (0.1%)	1177 (8.5%)
E	6 ^d	77.9	19 773	1459 (8.2%)	44 (0.2%)	22 (0.1%)	1922 (9.7%)
F	5	55.8	14 653	1177 (9.9%)	124 (0.8%)	68 (0.5%)	2581 (17.6%)
G	5	74.0	13 624	993 (8.0%)	87 (0.6%)	54 (0.4%)	1047 (7.7%)
H	5	77.5	16 023	588 (3.9%)	465 (2.9%)	15 (0.1%)	480 (3.0%)
I	4	84.0	10 887	659 (6.6%)	226 (2.1%)	7 (0.1%)	710 (6.5%)
J	4	83.0	12 424	846 (7.3%)	36 (0.3%)	23 (0.2%)	713 (5.7%)
Total	51	796.8	160 893	8886 (6.1%)	1619 (1.0%)	277 (0.2%)	12 775 (7.9%)

^aFor operations where capture effort was not recorded daily, the number of trap nights was estimated by multiplying the number of traps set on the first night by the number of nights trapped.

^bPer cent capture rate calculated as the number of badgers caught and despatched per available trap per night, where available traps are defined as those not disturbed and not occupied by another species.

^cPercentages calculated as the proportion of all trap nights affected.

^dIncludes two operations conducted in one culling year.

Table 2 Capture rate, and interference with trapping, on culling operations conducted in reactive areas

Triplet	Number of operations ^a	Total trap nights	Number (%) animals caught		Number (%) trap nights disrupted	
			Badgers ^b	Other species ^c	Badgers released	Other interference
A	7	1600	84 (5.4%)	29 (1.8%)	1 (0.1%)	1 (0.1%)
B	5	3457	194 (6.0%)	56 (1.6%)	0 (0.0%)	169 (4.9%)
C	13	2595	216 (9.5%)	12 (0.5%)	8 (0.3%)	312 (12.0%)
D	4	1600	122 (7.7%)	7 (0.4%)	0 (0.0%)	2 (0.1%)
E	10	2468	188 (7.7%)	22 (0.9%)	1 (0.0%)	14 (0.6%)
F	10	3967	435 (11.8%)	9 (0.2%)	14 (0.4%)	271 (6.8%)
G	6	2549	256 (10.4%)	14 (0.5%)	1 (0.0%)	82 (3.2%)
H	4	1898	159 (9.1%)	75 (4.0%)	2 (0.1%)	73 (3.8%)
I	3	975	94 (10.0%)	10 (1.0%)	2 (0.2%)	19 (1.9%)
Total		21 109	1748 (8.8%)	234 (1.1%)	29 (0.1%)	943 (4.5%)

^aNumber of operations' refers to the number of culls for which capture effort data were available, not the total number of operations performed (see text).

^bPer cent capture rate calculated as the number of badgers captured per available trap per night, where available traps are defined as those not disturbed and not occupied by another species.

^cPercentages calculated as the proportion of all trap nights affected.

No reactive culling was performed in Triplet J.

badgers at a particular sett, even though traps had been placed there. On an average night, 6.1% of trapped setts in proactive areas and 3.4% of those in reactive areas, were thus affected.

Capture rates

After accounting for interference and capture of non target species, on the first night of culling operations badgers were found in 20.1% of the traps in proactive areas and in 30.2% of the traps in reactive areas. Capture rates declined rapidly after the first night (Fig. 1a), averaging 6.1% in proactive areas (Table 1) and 8.8% in reactive areas (Table 2).

Within the proactive treatment, Poisson regression revealed substantial variation in badger capture rates on different culling days, operations and trial area regions (Table 3). The number of badgers captured per operation declined on successive culls (Fig. 1b), while the proportion of badgers captured in the outer region of culling areas (≤ 1 km inside) increased (cull sequence \times region interaction, χ^2 48.87, d.f. 6, $P < 0.001$; Table 3). There was no similar variation in the spatial distribution of badger captures over the course of each operation (days since the start of operation \times region interaction, χ^2 6.87, d.f. 6, P 0.65). The proportion of traps unavailable to badgers (through interference or capture of non target species) did not influence the capture rates in this analysis (χ^2 0.002, d.f. 1, P 0.97).

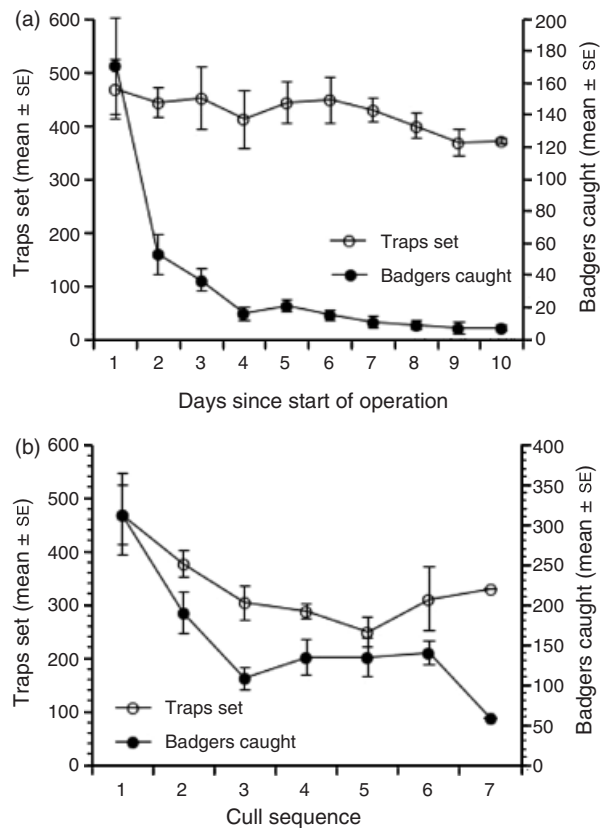


Figure 1 Variation in trapping effort and capture rate over time in proactive culling areas. (a) Numbers of traps set, and badgers *Meles meles* captured, on successive nights during initial proactive culling operations. (b) Number of traps set on the first night, and numbers of badgers caught (summed across all nights) for successive proactive culls. Data come from all operations for which data were available (see text).

Relationships between field signs and badger captures

Poisson regression revealed that the densities of badger field signs recorded on initial surveys were related to the numbers of adult badgers taken on initial culls from the same 4 km² squares (Fig. 2). Odds ratios indicate that a doubling (100% increase) in the density of field signs was associated with increases in adult captures of 92.9% [95% confidence interval (CI) 68.4–120.9%] for active setts, 43.4% (CI 20.8–70.2%) for main setts, 99.5% (CI 72.5–130.7%) for all setts, 84.7% (CI 63.8–108.3%) for active holes and 50.5% (CI 35.8–66.8%) for latrines ($P < 0.001$ in all cases).

Effects of culling on badger activity measured on field surveys

Before culling, the densities of badger field signs were comparable in areas subsequently allocated to the three treatments (Fig. 3). An unbalanced ANOVA comparing the densities of active setts across successive surveys, incorporating the effects of triplet, treatment (excluding reactive),

survey season and survey number, showed a significant treatment effect ($F_{1,67} = 44.1$, $P < 0.001$), with markedly lower sett densities in proactive areas (Fig. 3a); the treatment \times survey number interaction was not significant. By the fourth survey, the mean density of active setts in proactive areas ($1.29 \text{ km}^{-2} \pm 0.61 \text{ SD}$) was 59% lower than that in no culling areas ($3.16 \text{ km}^{-2} \pm 1.36 \text{ SD}$). Variation across triplets is shown in Fig. 4. By the fourth survey, the mean density of active setts in reactive areas ($2.77 \text{ km}^{-2} \pm 0.98 \text{ SD}$) was 17% lower than that in nine matched no culling areas ($3.34 \text{ km}^{-2} \pm 1.31 \text{ SD}$).

The number of active holes (all setts combined) per km² gives an alternative index of badger abundance (Fig. 2). On the fourth survey, the mean density of active holes in proactive areas ($2.83 \text{ km}^{-2} \pm 1.52 \text{ SD}$) was 69% lower than that in no culling areas ($9.18 \text{ km}^{-2} \pm 4.92 \text{ SD}$), and that in reactive areas ($7.23 \text{ km}^{-2} \pm 3.26 \text{ SD}$) was 26% lower than that in nine matched no culling areas ($9.81 \text{ km}^{-2} \pm 4.78 \text{ SD}$).

Latrine density showed a pattern similar to that for setts. An unbalanced ANOVA comparing latrine densities across successive surveys, incorporating the effects of triplet, treatment (excluding reactive) and survey number, showed a significant treatment \times survey interaction ($F_{4,66} = 4.54$, $P = 0.003$), indicating different temporal patterns in the two treatments. Latrine density declined markedly in proactive areas, but not in no culling areas (Fig. 3b). By the fourth survey, the mean latrine density in proactive areas ($2.49 \text{ km}^{-2} \pm 1.50 \text{ SD}$) was 73% lower than that in no culling areas ($9.14 \text{ km}^{-2} \pm 5.26 \text{ SD}$), and the latrine density in reactive areas ($7.09 \text{ km}^{-2} \pm 4.55 \text{ SD}$) was 26% lower than that in the nine matched no culling areas ($9.56 \text{ km}^{-2} \pm 5.39 \text{ SD}$). Survey season did not explain variation in latrine density in this analysis ($F_{3,76} = 0.35$, $P = 0.79$).

Effects of culling on badger activity measured by bait marking

The numbers of bait returns per km² appeared to be influenced by culling (Fig. 3c). Bait return density inside proactive areas was on average 64% lower than that in matched no culling areas (range 36–76% lower) and 76% lower than that in adjoining uncultured areas (range 75–77%). Reactive culling was associated with a 53% reduction in bait return density.

Effects of culling on retrieval of road-killed badgers

Culling also influenced retrieval rates of badgers killed in road traffic accidents. In the road traffic accident survey as a whole, carcass retrieval rates increased over time, largely due to increasing effort (Fig. 3d). The same pattern was observed in no culling areas, and around proactive areas, but not inside proactive areas where retrieval rates were consistently low (Fig. 2d). A Poisson regression analysis of the numbers of carcasses retrieved in proactive and no culling areas (including triplet, area, year and treatment as covariates) showed a significant treatment \times year

Table 3 Predictors of the numbers of badgers captured in the inner and outer regions of proactive culling areas, revealed by Poisson regression

Predictor	Odds ratio (95% CI)	χ^2	d.f.	P
Triplet		467.8	9	<0.001
Cull sequence (initial to seventh)		111.1	6	<0.001
Days since start of operation		2900	9	<0.001
Traps available (ln transformed)	1.34 (1.22 1.47)	40.66	1	<0.001
Area accessible (ln transformed)	3.20 (1.85 5.51)	17.94	1	<0.001
Active setts (ln transformed)	1.28 (1.12 1.46)	13.24	1	<0.001
Season		44.84	2	<0.001
Summer versus winter	1.41 (1.27 1.56)			
Autumn versus winter	1.24 (1.09 1.42)			
Region (outer or inner)		0.04	1	0.84
Cull sequence \times region		48.87	6	<0.001
Outer versus inner				
Initial cull	1.61 (0.89 2.89)			
Second cull	1.57 (0.88 2.81)			
Third cull	2.24 (1.25 4.02)			
Fourth cull	2.51 (1.40 4.48)			
Fifth cull	2.45 (1.36 4.42)			
Sixth cull	2.07 (1.13 3.81)			
Seventh cull				

Data are from the period when details of capture effort and success were recorded for every sett trapped (June 2002 to October 2006).

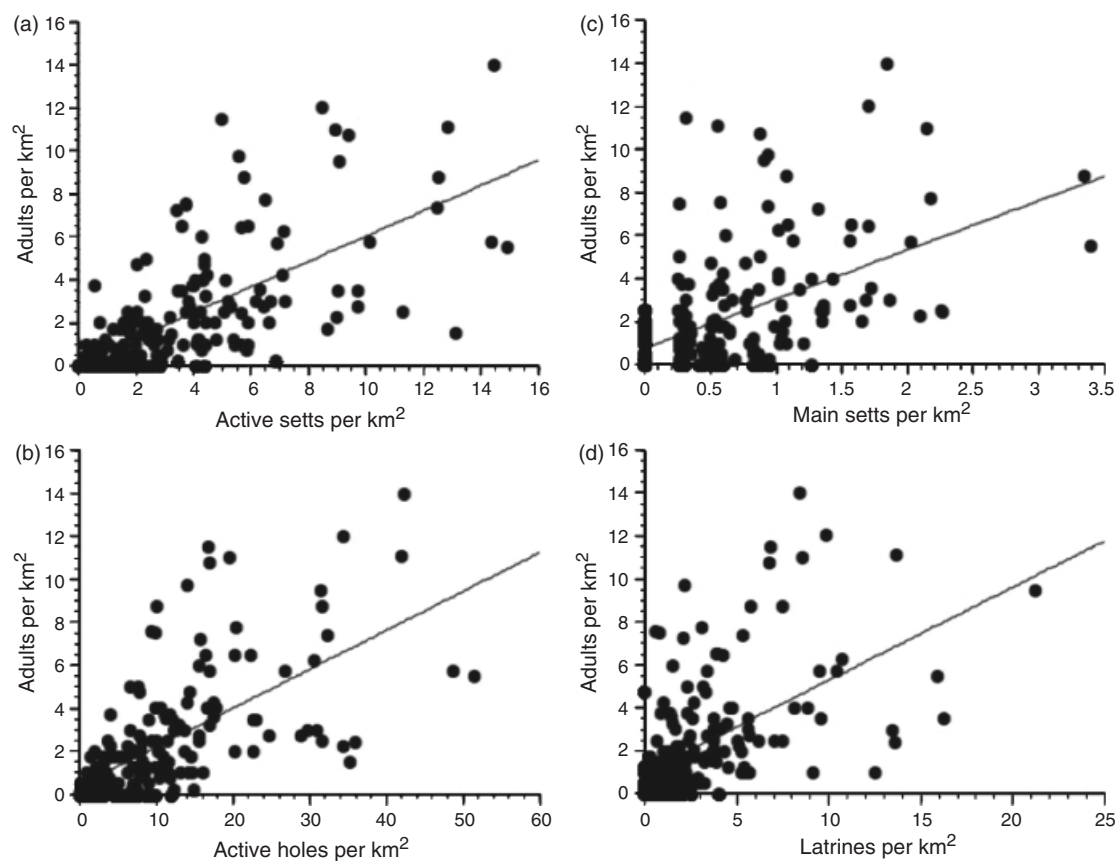


Figure 2 Relationships between the densities of badger *Meles meles* field signs and the numbers of badgers captured. Graphs compare the densities of adult badgers captured on initial culls, in 2 \times 2 km grid squares, with the corresponding densities of (a) active setts, (b) active holes, (c) main setts and (d) latrines recorded on initial (pre cull) surveys.

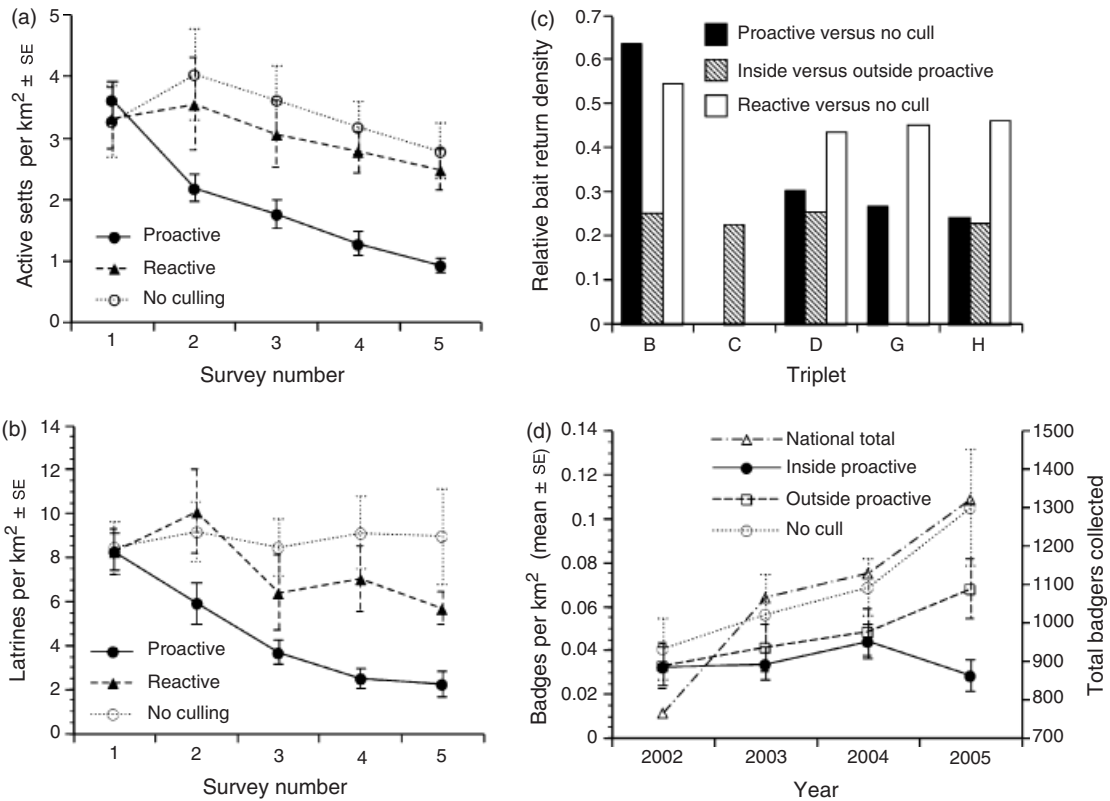


Figure 3 Effects of culling on indices of badger *Meles meles* activity. Graphs indicate the densities of (a) active setts and (b) badger latrines recorded on successive field surveys. Reactive culling was suspended immediately before the second survey in two triplets, and between the second and third surveys in the remaining seven triplets (no reactive culling occurred in Triplet J); there is no evidence of subsequent recovery of the badger population. Graph (c) shows the densities of bait returns in culling areas, expressed relative to the densities recorded in matched areas not subjected to culling, in five triplets where badger home ranges were mapped by bait marking. Graph (d) shows the total numbers of road killed badgers retrieved nationally, and numbers retrieved per km² inside, and up to 5 km outside, seven proactive culling areas and inside matched no culling areas.

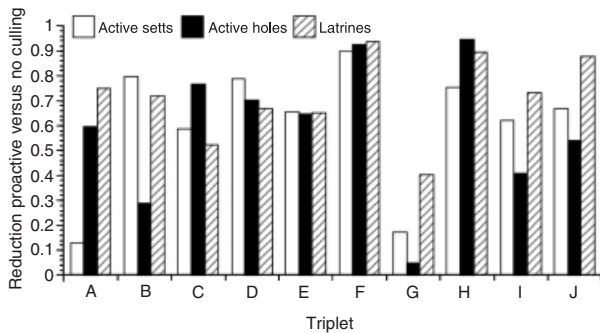


Figure 4 Consistency of proactive culling effects across triplets. Effects on field sign densities were estimated by calculating, for each trial area, the proportional change in density between the first and the fourth survey, and then comparing this change in proactive and no culling areas.

interaction ($\chi^2 = 11.94$, d.f. = 3, $P = 0.008$), reflecting these different temporal patterns in the two treatments. By 2005, the average density of road killed badgers retrieved inside seven proactive culling areas ($0.029 \text{ km}^{-2} \pm 0.017 \text{ SD}$) was

73% lower than that recorded in the corresponding no culling areas ($0.105 \text{ km}^{-2} \pm 0.027$), and 58% lower than that recorded in the 5 km zone surrounding proactive areas ($0.068 \text{ km}^{-2} \pm 0.014$). In 2003, the last year of reactive culling, the average density of road killed badgers was 9.8% lower inside six reactive areas ($0.061 \text{ km}^{-2} \pm 0.023 \text{ SD}$) than in six matched no culling areas ($0.068 \text{ km}^{-2} \pm 0.037 \text{ SD}$).

Discussion

The data presented here reveal substantial effects of culling on all indices of badger abundance, consistent with the original aims of the RBCT (Bourne *et al.*, 1998). For example, proactive culling was associated with a 73% reduction in latrine density, a 69% reduction in the density of active holes, a 64% reduction in the density of bait returns and a 73% reduction in the density of road killed badgers. Different indices provided roughly comparable estimates within each triplet (Fig. 4). While the density reductions achieved by proactive culling varied across triplets, these appeared not to reflect variation in the overall rates of capture or interference (Table 1) or the efficacy of

initial proactive culls as estimated by Smith & Cheeseman (2007).

Activity reductions associated with reactive culling were smaller than those for proactive culling: average values were 26% for latrine density, 32% for active hole density, 53% for bait returns and 10% for road kill density. Interestingly, indices provide no evidence of population recovery following suspension of the reactive strategy (Fig. 3).

All measures indicate substantial effects of culling on badger population densities, but the precise magnitude of the effect is difficult to measure using these methods. Although the densities of field signs were correlated with the numbers of badgers taken on initial culls (Fig. 2), these relationships cannot be used to calibrate the density indices because the relationship between capture rate and true density is unknown. New methods have been developed recently for directly (Hounsome *et al.*, 2005) and indirectly (Tuytens *et al.*, 2001; Wilson *et al.*, 2003a,b; Frantz *et al.*, 2004) enumerating badgers, but these were developed after the start of the RBCT and so could not be used to measure temporal trends.

Despite the limitations of the survey methods available, the broad consistency of our findings across multiple methodologies is reassuring. In culled areas, the number of setts used by each badger is elevated (Cheeseman *et al.*, 1993), while the use of latrines is reduced (Hutchings, Service & Harris, 2002); such behavioural changes probably contributed to the variation between measures of culling impacts shown in Fig. 4.

The proportion of badgers caught close to the culling area boundary increased on successive proactive culls. This provides evidence of immigration into the areas cleared by culling, and is consistent with the evidence of population reduction immediately outside culling area boundaries documented by Woodroffe *et al.* (2006a). This evidence of immigration shows that the indices of local badger activity were probably generated by populations comprising new immigrants as well as animals missed by culling operations. Hence, while field signs provide valuable indicators of the broad reductions in badger density achieved by culling, they almost certainly underestimate the proportion of the original population that was removed.

Reproduction was more important than immigration in the repopulation of a smaller area cleared by culling at Woodchester Park (Cheeseman *et al.*, 1993). In our proactive areas, however, repeated culling would have countered population growth through breeding. It is likely that the proactive areas functioned as 'sink' patches influencing population dynamics over larger areas, as has been described for several other species (Mace & Waller, 1998; Woodroffe & Frank, 2005). This 'vacuum effect' has been linked to elevated prevalence of *M. bovis* infection in badgers close to culling area boundaries, and increased TB incidence in neighbouring cattle (Woodroffe *et al.*, 2006b). Culling methods such as snaring and gassing, which have been considered for future use because of their potentially greater efficiency at removing badgers (Defra, 2005), are likely to have similar or greater consequences for source

sink dynamics. Such methods could therefore be expected to generate 'edge effects' on disease similar to those documented in the RBCT.

Interference with culling activities occurred on all proactive and many reactive culling operations. However, the level of interference was not found to explain variation in the numbers of badgers captured.

Taken together, our analyses indicate that proactive culling substantially reduced badger population densities. Nevertheless, this treatment reduced overall cattle TB incidence by only 19% (95% CI 6.2–30%, Donnelly *et al.*, 2006). Immigration into culled areas, along with disruption of social and territorial organization, appears to cause increased contact among badgers and hence elevated *M. bovis* prevalence (Woodroffe *et al.*, 2006a,b). This increased prevalence, combined with expanded ranging behaviour likely to increase contact between badgers and cattle herds (Woodroffe *et al.*, 2006a), may explain the limited capacity of substantial badger population reduction to achieve comparable reductions in TB risk for cattle.

The reductions in badger population density described here were achieved by a systematic and coordinated effort, conducted by specialist staff and sustained over several years. Any culling policy developed in future would probably need to be conducted with a similar, or greater, intensity and would therefore require comparable effort. Even if culling efficiency could be improved somewhat, modelling suggests that further reductions in cattle TB incidence could be marginal (Smith *et al.*, 2001; Cox *et al.*, 2005), and detrimental edge effects would still be likely. Because substantial reduction of badger populations over wide areas requires massive effort, generates only modest reductions in cattle TB incidence in culled areas and elevates cattle TB incidence in neighbouring areas, this approach appears to have limited value for TB control in British cattle.

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