COST-BENEFIT ANALYSIS MODEL OF BADGER (MELES MELES) CULLING TO REDUCE CATTLE HERD TUBERCULOSIS BREAKDOWNS IN BRITAIN, WITH PARTICULAR REFERENCE TO BADGER PERTURBATION

Authors: Wilkinson, D., Bennett, R., McFarlane, I., Rushton, S., Shirley, M., et al.

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COST-BENEFIT ANALYSIS MODEL OF BADGER (*MELES MELES*) CULLING TO REDUCE CATTLE HERD TUBERCULOSIS BREAKDOWNS IN BRITAIN, WITH PARTICULAR REFERENCE TO BADGER PERTURBATION

D. Wilkinson,[1,4] R. Bennett,[2] I. McFarlane,[2] S. Rushton,[3] M. Shirley,[3] and G. C. Smith[1]

[1] Food and Environment Research Agency, Sand Hutton, York YO41 1LZ, UK
[2] Department of Agricultural and Food Economics, University of Reading, PO Box 237, Reading RG6 6AR, UK
[3] Division of Biology, Newcastle University, Newcastle NE1 7RU, UK
[4] Corresponding author (email: david.wilkinson@fera.gsi.gov.uk)

ABSTRACT: Bovine tuberculosis (TB) is an important economic disease. Badgers (*Meles meles*) are the wildlife source implicated in many cattle outbreaks of TB in Britain, and extensive badger control is a controversial option to reduce the disease. A badger and cattle population model was developed, simulating TB epidemiology; badger ecology, including postcull social perturbation; and TB-related farm management. An economic cost-benefit module was integrated into the model to assess whether badger control offers economic benefits. Model results strongly indicate that although, if perturbation were restricted, extensive badger culling could reduce rates in cattle, overall an economic loss would be more likely than a benefit. Perturbation of the badger population was a key factor determining success or failure of control. The model highlighted some important knowledge gaps regarding both the spatial and temporal characteristics of perturbation that warrant further research.

Key words: Badger, bovine tuberculosis, cattle, economics, *Meles meles*, *Mycobacterium bovis*, spatial model.

INTRODUCTION

Bovine tuberculosis (TB), caused by *Mycobacterium bovis*, is zoonotic and a serious economic problem in parts of the world (Grange, 2001; Smith et al., 2004). It has become particularly serious for the British farming industry in which the number of cattle herd breakdowns (CHBs: the detection of TB in a cattle herd) has risen steadily since 1990, particularly in the southwest (Donnelly et al., 2003). In Great Britain in 1997, the government reported spending £16.0 M on bovine TB surveillance, control, and research, but by 2003/2004, this had risen to £88.2 M (unpubl. data). Between 2004 and 2007, the annual expenditure varied between £80M and £100M.

The European badger (*Meles meles*) is often infected with TB (Delahay et al., 1998), and there is now conclusive evidence that they are responsible for transmission of disease to cattle (Independent Scientific Group, 2007). To date, no proven vaccine can be used to protect against bovine TB, either in badgers or in cattle, and since 1970, various control regimes have been tried, mainly based on culling the badger population. However, the incidence of TB in cattle has continued to rise. Among the potential reasons why badger culling might not work (Delahay et al., 2003) is the proposition that the social perturbation of badger social groups after culling could increase the rate of TB spread (Swinton et al., 1997; Tuyttens et al., 2000). Analysis of the results of the Randomized Badger Culling Trial (RBCT) added further evidence of disease exacerbation in areas surrounding badger removal (Donnelly et al., 2003, 2007). Indeed, part of the trial was suspended because one control strategy (reactive culling) was proven to be increasing the CHB rate (Donnelly et al., 2003). Perturbation of badger social groups was proposed as the most likely explanation.

Conversely, in a large trial in Ireland (Griffin et al., 2005), a substantial reduction in the CHB rate was observed in areas where badgers had been culled extensively. However, it is possible that because badgers in the Irish trial were culled in large areas with natural barriers (sea or mountain), badgers were not able to migrate into the culled areas, and social perturbation in surrounding areas would have been minimized.

The RBCT also highlighted just how expensive badger control can be, particularly in terms of labor and equipment outlay, such as purchase of badger cage-traps, although the costs were less in Ireland, where snares were used. The economic risks of a badger or cattle management strategy or a management strategy for both should be assessed before implementation.

In this study, we aimed to provide evidence to inform TB management decisions by modeling a badger population, a cattle population, TB disease dynamics, and the costs and benefits. A further aim of this study was to assess the importance of social perturbation on both the disease dynamics in badgers and cattle and its effects on cost-benefit, to assess whether the perturbation process, as modeled, can be considered a close enough representation of what happens in the field and to identify knowledge gaps in the processes that warrant further research.

MATERIALS AND METHODS

Model design

An individual-based spatial stochastic badger/TB model was used (Smith et al., 2001a, b; Wilkinson et al., 2004). To this, a cattle layer was added to the model so that spatially realistic interactions and TB transmission between badgers and cattle could be simulated. The model time step was reduced to 2 mo so that farm management (such as TB testing) could be better simulated.

The badger and cattle layers are both modeled on a 100×100 grid, each cell of which represents 200×200 m (total grid area represents 400 km^2). The grid was wrapped to form a torus to eliminate edge effects. Model parameter settings were based on means from an area of six counties in the South West of England (Avon, Cornwall, Devon, Gloucestershire, Hereford and Worcester, and Wiltshire), that comprises mixed farmland with high densities of badgers and cattle and a high CHB rate. Badger main setts were distributed randomly over the landscape at a density of 1.3 setts/km^2, and badger territories were created by tessellation, each grid square assigned to the closest main sett. Each badger territory was assigned a carrying capacity (maximum number of breeding females) to limit population growth. Cattle grazing land was created by distributing farms at random over the landscape at a density of 0.78 farms/km^2 and then forming a grazing area within each farm, positioned at random, appropriately sized, and allocated as a beef, dairy, or mixed herd. In the model, the badger territories were fully contiguous, whereas only some of the cattle grazing areas were in direct contact with a neighboring herd. A proportion of badgers and cattle were initially infected with TB at random, and the model was run for a number of years to allow the disease to stabilize. Disease spread was simulated with specified transmission probabilities: within badger group, between badger groups, within cattle herd, between cattle herds, badgers to cattle, and cattle to badgers. Disease transmission was density dependent in the sense that each possible contact between each individual is given a fixed probability of TB transmission. A new spatial configuration and new initial populations (badger and cattle) were created for each iteration.

Management options

The primary effect of bovine TB on the cattle farming industry is the number of cattle testing positive for TB (reactors); the number of CHBs, each CHB affecting a farmer in many detrimental ways; and CHB rates, which if too high, potentially have effects on exports and the British economy. Thus, the CHB rate was used as the primary output and measure of strategy success. The financial consequences of each CHB and numbers of reactors were included in the cost-benefit section of the model. The focus on badger control to reduce TB in the short to medium term is just one of several strategies being looked at by politicians and the farming industry, but it is a complex strategy, in which modeling can play a particularly valuable role. A spatial layer was created to simulate parish areas, in that these serve as the basis for cattle management (e.g., TB testing frequency) and thus define the areas for badger control. Parishes created by tessellation varied in size (mean≈13 km^2).

A variety of different badger control options are possible in the model. The areas selected for control (seven parishes approximating one quarter of the grid area: 100 km^2) was determined from the emergent herd breakdowns in cattle. Those parishes with a history of higher numbers of CHBs were selected for badger control, and each control option was run from the same starting point conditions as the no-control option so that a true comparison could be made. The badger control options simulated were shooting, trapping, snaring, and gassing. To study the factors affecting the success of the control strategies, both in terms of reducing CHBs and the cost-benefit analysis, the efficacy of badger control (the proportion of badgers removed each year) and the proportion of land accessible for control (the farmer/landowner compliance) were varied. In the RBCT, traps were set at the edge of noncompliant land within the culling area to catch badgers from setts that were otherwise not available for trapping. Trial results demonstrated that badgers could be successfully culled from noncompliant land; presumably access to part of the territory is sufficient to cull many individuals. In the model, we assumed that if at least 10% of a social group territory was accessible for culling, then badgers could be removed at the same rate as if 100% was accessible. The effects of increasing the grid size and the area designated for badger control (200 and 300 km^2) also were investigated.

Cattle movements were simulated so that about 40% of cattle moved each year (on the basis of Cattle Tracing Scheme data (Mitchell, Veterinary Laboratories Agency, pers. comm.). Priority was given for young males to move to beef units and females to dairy, and distances moved were minimized wherever possible to simulate the likely market movement patterns seen in reality. If a herd was short or had excess cattle in terms of its ideal stocking density, extra movements were simulated to redress the balance.

Bovine tuberculosis testing of cattle was modeled to simulate the regime applied in reality. Cattle were tested routinely at a testing interval determined by the local CHB rate. The testing interval of each parish (one, two, three, or four times yearly) was reassessed annually with the use of the same decision process used in real life. The detection of TB during the testing regime was determined probabilistically to simulate the limited sensitivity of the TB skin test, and a positive test triggered slaughter, postmortem examination of the reactors, and movement restrictions plus follow-up testing of the contacts, as happens in reality.

Density dependence

Badgers in groups below carrying capacity can have reduced mortality rates (Cheeseman et al., 1993). To simulate this, density-dependent mortality rates were introduced at the social group level (see Appendix C.1). Earlier models also assumed that only females aged 3 yr or more were able to breed. Because it is possible for 2-yr-old females to breed (Cresswell et al., 1992), the 2-yr-old females in the model also were allowed to breed when there was a shortage of older females. Density-dependent fecundity at the social group level also was included (see Appendix C.1). With these density-dependent changes, simulated population recovery rates were comparable to those experienced in the field (unpubl. data).

Social perturbation of badgers

Social perturbation of badgers after population control comprises two aspects of the model: 1) badgers are allowed to move into nearby social groups that contain few or no badgers, and 2) badger TB transmission rates are increased in areas where, and close to where, culling has occurred.

The extra movement process is in addition to normal badger dispersal and can occur at any time, whether or not badger culling has occurred. This allows recolonization of badger territories that are stochastically going extinct and also allows substantial immigration of badgers into culled areas (see Appendix E; 12, 13). In the model, a badger could potentially move two social groups each time step, equating to several kilometers over a year. The immigration distances simulated by the perturbation routine were thus comparable to those seen in the field after culling (Carter et al., 2007). Badger-to-badger TB transmission rates were increased in culled areas and nearby territories by assuming that contact between animals in adjacent territories became similar to those within a territory (i.e., increasing between-group transmission rates to equal those of within-group transmission rates) to simulate higher contact rates that occur as a result of the extra roaming of surviving badgers (Cheeseman et al., 1988). Two questions arise when modeling social perturbation. The first is how far the effect reaches beyond the badger control area, and the second is how long the effect persists after the culling has stopped. Two different extents of "perturbation reach" were tested in the model: the first with all the culled badger social groups plus one ring of neighboring groups (single-ring perturbation) and a second with the culled groups plus two rings of neighbors (double-ring perturbation). For direct comparison with the RBCT results, the model's CHB rates were output specifically for three areas: 1) the core area, defined as two or more kilometers inside the cull area; 2) the inner zone, defined as the area between the core and the cull boundary; and 3) the outer zone, defined as the area up to 2 km outside the cull boundary. (Results from the RBCT demonstrated that badger culling appeared to increase the CHB rate significantly outside the culling boundary—the so-called "edge effect.")

The second question was how long the perturbation effect lasts once culling stops. Bait-marking studies suggested that perturbation can last for up to 10 yr after a cull (Cheeseman et al., 1993), but it was thought likely that the intensity of the perturbation effects significantly reduces within the first 5 yr. We assumed for this model that the increased transmission rates would begin at the start of culling, continue until 3 yr after the final cull, and then abruptly switch off (i.e., return to normal rates).

To study the relative importance of different aspects of perturbation, the model also was run with the "increased transmission rates" feature of perturbation switched off and with control applied to the whole grid to remove the edge effects of perturbation. The latter prevented immigration of badgers into the culled area.

Premovement testing of cattle

Premovement testing (PrMT) of cattle was introduced in England in March 2006 to try and limit the spread of undiagnosed TB into new areas. This required that, in areas already subjected to routine TB tests every 1 or 2 yr, cattle over a certain age had to have a recent negative TB test before being allowed to move from one farm to another. Premovement testing of cattle was included as a default in the model to simulate the practice used in the field and was applied for long enough that population and disease dynamics had stabilized before badger control was started.

Cost-benefit analysis

A partial cost-benefit analysis was integrated in the model to allow a Net Present Benefit (NPB) value for each control option to be calculated for each simulation. During each simulation, a no-control option was run, during which comprehensive costs were accumulated (testing cattle for TB, slaughtering and disposing of TB reactor cattle, cattle movement restrictions imposed on herds in which TB is confirmed or suspected, follow-up tests and isolation of cattle that have inconclusive test results, and PrMT of cattle). Costs were obtained from the Department for Environment, Food, and Rural Affairs (unpubl. data) and survey results (Appendix D).

Following each no-control run, the model population and disease states were reset to the start point and the model rerun, but with a badger control option included. As well as cattle management costs, badger control costs also were then accumulated (equipment purchase, badger sett surveys, labor, and badger carcass disposal). For this model, it was assumed that most badger control costs were borne by the farmer/landowner. This approach was optimistic because those costs are lower than government staff labor costs would be, but it also reflects possible policy and was a good starting point, because if a control strategy is not economically viable with lower costs then it certainly will not be with higher costs. The economic value of badgers as perceived by the public has been studied (Bennett and Willis, 2007), but those studies were limited in scope and had not considered the effects of the method of killing a badger on its value to the public. Our study, for simplicity, did not consider the value that the public might put on badgers existing and not being killed, nor did it consider the nonfinancial costs to farmers of having a CHB, although both those aspects are likely to need careful consideration by policy makers.

By comparing accumulated discounted costs of each control option with no control, an NPB was calculated for each control scenario. Any changes in the CHB rate resulting from badger control would thus feed through to the NPB. Because each simulation of the stochastic model resulted in a separate NPB value, the distribution of the NPB values represented the risk of the control strategy; a majority of positive NPBs indicated a high chance of economic gain, and a majority of negative NPBs indicated a high risk of economic loss.

Variables and inputs

Default parameter values were taken from previous model versions and available field data (Appendices A–D). Where possible, all badger parameters were derived from a single study population (Woodchester Park, southwest England; see Rogers et al., 1997, 1998; Delahay et al., 2000; Wilkinson et al., 2000). Badgers were characterized by the following variables: social group, sex, age, and TB status. The age categories were juvenile, yearling

(1 yr old), and adult. The TB status categories (Delahay et al., 2000) were defined healthy, infected, infectious, and superinfectious (persistently excreting TB bacilli). Badger fecundity in the model was density dependent on the basis of a heterogeneous threshold carrying capacity (mean upper threshold of three litters per social group) set at random for each social group (Smith et al., 2001b). Litter size was modeled probabilistically from a distribution of known litter sizes (Neal and Cheeseman, 1996), with a mean of 2.94 cubs/litter and a sex ratio of 1:1. Mortality rates were taken from Wilkinson et al. (2000). Badgers were allowed to disperse to smaller social groups, if available, on the basis of sex-dependent probabilities (males more often than females), independent of age and season.

Cattle population parameters (number of dairy and beef farms and stocking densities) were derived from the UK June Census 2004 dataset (Defra, unpubl. data), cattle mortality (slaughter) rates from the Cattle Tracing Scheme (CTS) 2002 to 2004 dataset, and the cattle TB disease parameters and CHB rates from the UK VetNet dataset. Cattle were characterized by the variables herd, sex, age (30×2-mo categories with the last category also used for older cattle), and TB status (healthy, infected, infectious, superinfectious). Superinfectious cattle were defined as heavily infectious yet anergic (not responding to the TB skin test). All female cattle aged over 22 mo gave birth to one calf annually. The sex ratio of the calves was set to 1:1. Herds were categorized as beef or dairy, and parameter values varied according to herd type. Stocking density distributions from the June Farm Census were dependent on herd type and were used in the model to allocate a stocking density to each farm.

Bovine tuberculosis transmission rates for badgers and cattle were adjusted so badgers directly contributed to about 60% of CHBs (when PrMT was in effect), prevalence of TB in the badger population (before control) stabilized to about 18%, and the mean CHB rate stabilized at about 8% of farms per year. Analysis of the VetNet disease data records (unpubl. data) indicated that the CHB rate per unit area had been stable at about this level in the severely affected areas between 2003 and 2005. Between-group badger transmission rates were set to one twentieth of the within-group rates to simulate the spatial and temporal occurrence of diseased social groups. Likewise, between-herd rates were set to be one twentieth of the within-herd rates. Within-herd transmission rates for beef herds were set twice as high as those for dairy, following the findings of Munroe et al. (2000). The standard TB test sensitivity was set at 70% (Goodchild, UK Veterinary Laboratories Agency, pers. comm.) and increased to 90% to simulate the more severe interpretation of the skin test reaction used when a positive was confirmed at postmortem. Test specificity was set to 99.7% (standard interpretation) and 99.9% (severe interpretation) (Goodchild, UK Veterinary Laboratories Agency, pers. comm.). Efficacy rates for badger removal were set to 50% for shooting, 70% for trapping (Smith and Cheeseman, 2007), and 80% for snaring or gassing. These control rates were before land compliance rates were factored in. Control of 80% was believed to be a reasonable upper level achievable for widespread control, even with snaring or gassing. In Ireland, badger snaring was recently assumed to be 85% effective (Sleeman et al., 2009), only marginally above our assumption.

Model scheduling

Because we were modeling an area with a severe cattle TB problem that nevertheless seemed to be stable (see previous section), rather than the initial spatial spread or rise in disease prevalence, the processes of which are poorly understood, it seemed sensible to model badger control from a stable disease level. To establish such stability, 135 yr were simulated in the model (with the final 15 yr analyzed economically), and several processes were introduced sequentially to allow population and disease dynamics to stabilize. The year labeled 0 on the graphs (for clarity) was preceded by 115 simulated yr to ensure stabilization of various metrics. First, the grid was populated with badgers and cattle, seeded with TB infection, and allowed to stabilize for 30 yr. All parishes had a TB test interval of 1 yr for the first 50 yr of each simulation and thereafter changed test intervals according to CHB history in each parish. Premovement testing of cattle was simulated from year 100 onward, and badger control was applied annually in years 120 to 124 inclusive (years 5 to 9 on the rescaled graphs).

Within each time step (six times per year, or as otherwise stated) model processes occurred in the following order: 1) births of badgers (time step 1 only=February); 2) aging of badgers (time step 1 only=February); 3) births of cattle; 4) mortality of badgers; 5) mortality of cattle (sent to slaughter); 6) dispersal of badgers; 7) culling of badgers (years 120 to 124 inclusive, and time step 3 only=June); 8) social perturbation of badgers; 9) movement of cattle (farm to farm),

Table 1. The percent change in cattle herd breakdowns after control (compared with no control) within and outside 100-km^2 badger cull areas measured in the randomized badger culling trial; and the equivalent output from model simulations of control by trapping, with implementation of (a) the single-ring perturbation rule and (b) the double-ring perturbation rule (further details in text). The Randomized Badger Culling Trial (RBCT) field data (first two rows) are taken from Donnelly et al. (2007) (95% confidence intervals in parentheses).

	Outer zone: 2-km ring outside the cull boundary (no control)	Inner zone: 2-km ring inside the cull boundary (control)	Core zone: an area >2 km inside the cull boundary (control)
RBCT (actual field) based on VetNet location data	24.5 (−0.6, 56.0)	−23.2 (−32.7, −12.4)	
RBCT (actual field) based on RBCT location data	35.3 (5.8, 73.0)	−17.4 (−27.2, −6.2)	
Model with single-ring perturbation rule	−9	−18	−37
Model with double-ring perturbation rule	20	−9	−33

including PrMT of cattle, if included; 10) spread of TB infection—first badger-to-badger, then cattle-to-cattle, badger-to-cattle, and cattle-to-badger; 11) TB disease progression in badgers; 12) TB disease progression in cattle; 13) cattle testing (routine testing of cattle for TB, if due for herd); 14) aging of cattle; 15) output data (time step 6 only—end of each year). The processes (submodels) are described in detail in Appendix E.

Outputs

The output parameters calculated at the end of each simulated year were badger population size, badger epidemiology (number infected and prevalence), CHB rates, costs of each control (Net Present Values), and control benefits compared with no control. Most outputs were summarized across the simulations, but a discounted net benefit value was output for each simulation so the economic variation could be illustrated. Output metrics were calculated for the whole grid area, so these represented averaged values across both the noncontrolled portion of the grid (~75% of the grid) and the controlled area (~25% of the grid). It was important to include areas outside the control boundary, so factors such as perturbation, which can affect the economics, were included in the analysis. However, the area simulated and the proportion being controlled were taken into account in interpreting the results.

RESULTS

A comparison of the spatial effects between the model and the RBCT is summarized in Table 1. This comparison shows that simulating a single ring of perturbation failed to give the "edge effect" increase in CHBs, but applying the double-ring rule gave a reasonable match of the spatial CHB profile—the model giving a 20% increase in the outer zone, and the RBCT giving an increase of between 24% and 35%. The double-ring perturbation rule was therefore used in all subsequent simulations. Unless otherwise stated, results are from the model run with the following default settings: 1) badger control started in year 5 and finished in year 9 on the graph scale presented, 2) social perturbation (where triggered) started in year 5 and finished in year 12, 3) the control area was 100 km^2, and 4) land access compliance was 70%.

Badger population

The modeled badger population, represented by mean badger group size, remained stable at 7.5 adult badgers per social group when no badger control was applied. The population was significantly reduced by all culling methods during the five control years and then recovered during the following 10 yr. The amount of population depression was proportionate to the effectiveness of badger removal, reaching a mean minimum social group size of 4.6 after 5 yr of culling at 80% per annum.

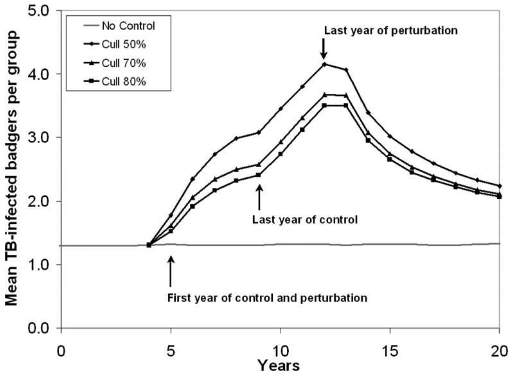

FIGURE 1. The effect of different badger culling efficacies on the modeled number of bovine tuberculosis (TB)–infected badgers per group.

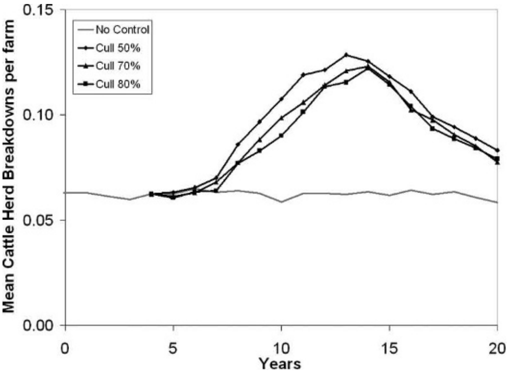

FIGURE 2. The effect of different badger culling efficacies on the modeled mean annual cattle herd breakdown rate.

Badger TB prevalence

The model output for badger TB prevalence remained stable at about 18% when no badger control was applied. The badger control options all showed similar trends, with an initial rise in prevalence in year 5 due to the perturbation effect of culling. Prevalence continued to rise to a peak in year 12 (maximum 60% to 70%) and then declined once the perturbation effect had been switched off in the model. Culling methods with lower cull rates gave greater rises in prevalence throughout the whole period.

Infected badgers

The actual number of infected badgers remaining after a cull should be a good measure of the badger TB risk to cattle. The mean number of infected badgers per social group remained stable at about 1.3 when no badger culling was being applied (Fig. 1). Badger control options showed similar trends to each other, with an initial rise in the numbers of infected badgers in year 6 as a result of perturbation. The number of infected badgers continued to rise to a peak in year 12 and then declined once the perturbation effect had been switched off. The option with the lower cull rate of 50% resulted in the highest rise in infected badgers throughout the whole period.

Cattle herd breakdowns

The model output for CHBs (Fig. 2) showed a very similar trend to numbers of infected badgers (Fig. 1) but with more variation. Without badger control, the mean CHB rate was about 6.3% of cattle herds because PrMT had caused some reduction. Badger culling caused an increase in the CHB rate when measured across the whole simulation grid, with the greatest increase being realized by the lowest cull rate (shooting). For the CHB rate, as for the numbers of infected badgers, the perturbation effect overrode the culling effect, and the rates had not returned to precull rates 8 yr after the perturbation effect was switched off.

Economics

All of the distributions of simulated NPBs for the cull strategies indicated that the economic outcome would be negative (i.e., the economic losses would outweigh any economic gains; Fig. 3). On the assumption that the modeled perturbation process is sufficiently close enough to what happens in the field, trapping badgers (70% removal) appears to be the worst option economically, with 100% of the simulations showing a net economic loss, and the magnitude of the losses being greater than the other culling options. This was mainly because of the high set-up cost

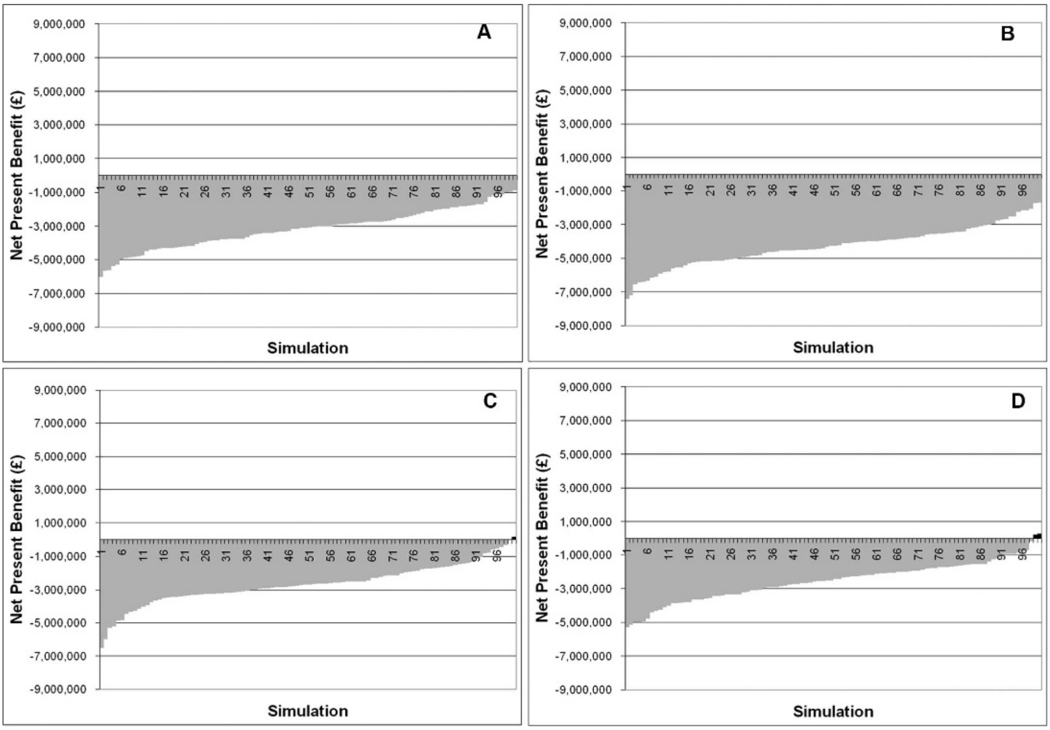

FIGURE 3. The effect of different badger control options on the discounted net benefit distribution. Each bar is the overall economic benefit of one simulation, taking into account the economics of the badger control, and cattle disease management. (A) Shooting (50% removal), (B) trapping (70% removal), (C) snaring (80% removal), (D) gassing (80% removal).

of trapping badgers. However, the economic benefit distributions of the shooting, snaring and gassing options were similar, with 100%, 99%, and 98% of simulations, respectively, giving a net economic loss.

Varying control rates

Increasing the control rates resulted in small reductions in the CHB rates relative to the low control rates (Table 2), but even the high rates of culling failed to counteract the perturbation effect sufficiently to bring the CHB rates down to the levels produced when no control was applied.

Varying control area

Increasing the control area resulted in small reductions in the CHB rates relative to the smallest area modeled (Table 3), and that effect was consistent across all the culling methods simulated. However, even

Table 2. Effect of control rates on mean annual cattle herd breakdown (CHB) rate per farm. The low control rates simulated for shoot, trap, snare, and gas were 30, 60, 70, and 70%, respectively; the medium rates, 50, 70, 80, and 80%; and the high rates, 70, 80, 90, and 90%. Means were calculated over 10 yr starting from the first year of culling.

	Mean no. of CHBs per farm				
Control rates	No control	Shoot	Trap	Snare	Gas
Low	0.063	0.097	0.081	0.077	0.078
Medium	0.063	0.086	0.078	0.074	0.075
High	0.063	0.078	0.074	0.073	0.073

Table 3. Effect of control area on mean annual cattle herd breakdown (CHB) rate per farm. Means were calculated over 10 yr starting from the first year of culling.

		Mean no. of CHBs per farm				
Control area (km^2)	Grid size (km^2)	No control	Shoot (50%)	Trap (70%)	Snare (80%)	Gas (80%)
100	400	0.063	0.098	0.092	0.087	0.089
300	1,024	0.063	0.086	0.078	0.074	0.075
400	1,600	0.063	0.080	0.073	0.071	0.071

culling badgers across 400 km^2 failed to counteract the perturbation effect sufficiently to bring the CHB rates down to the "no-control" levels.

Varying land access compliance

With the default "drawing-out" rule (if 10% of a badger group is accessible it can be culled as if 100% were accessible), the simulations showed that, within the range tested, the CHB rate was insensitive to the proportion of noncompliant land (Table 4). It should be noted that the randomly allocated parcels of noncompliant land were all farm-sized, whereas in reality there may be some large areas of noncompliance that could affect the outcome.

Varying perturbation

A high level of perturbation was simulated with the double-ring rule described above, which best reproduced the reported RBCT "edge effects" and which gave overall increases in the CHB rate after culling (Fig. 2).

When the model was run without the "increased transmission rates" feature of perturbation (so animals could immigrate into the culled area but contact rates were normal, as if social structure had reestablished immediately) the CHB rate reduced by about one third, and a significant reduction was still present several years after culling ceased. As a result of these lower CHB rates, 68% of the simulations showed an overall economic benefit with the most cost-effective culling method (gassing).

Preventing immigration into the culled area (Fig. 4) gave reductions in the numbers of CHBs of similar magnitude to those seen with standard transmission rates. This was analogous to choosing a control area surrounded by coastline or very wide rivers. When badger immigration was prevented, the economic benefit picture was improved, with 67% of the simulations of culling by gassing showing an overall economic benefit (Fig. 5) compared with only 2% showing an economic benefit (Fig. 3D). However, even with immigration prevented in the model, the trapping option (most costly) was still economically risky, with 79% of the simulations giving an overall economic loss.

DISCUSSION

Suppression of the simulated badger population after culling showed a steep

Table 4. Effect of farm access compliance on mean annual cattle herd breakdown (CHB) rate per farm. Means were calculated over 10 yr starting from the first year of culling.

	Mean no. of CHBs per farm				
Farm compliance (%)	No control	Shoot (50%)	Trap (70%)	Snare (80%)	Gas (80%)
60	0.063	0.086	0.078	0.076	0.075
70	0.063	0.086	0.078	0.074	0.075
80	0.064	0.086	0.077	0.075	0.075

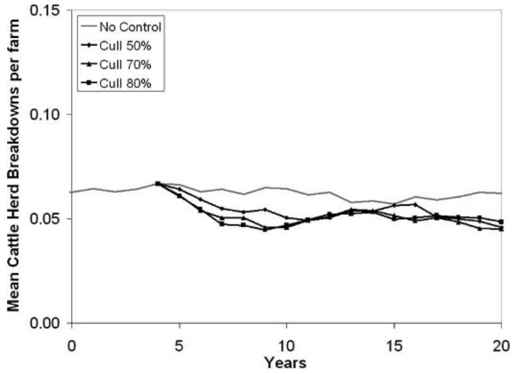

FIGURE 4. The effect of different badger culling efficacies on the modeled mean annual cattle herd breakdown rate. Badger control was applied annually from year 5 to 9, and immigration of badgers into the control area was prevented.

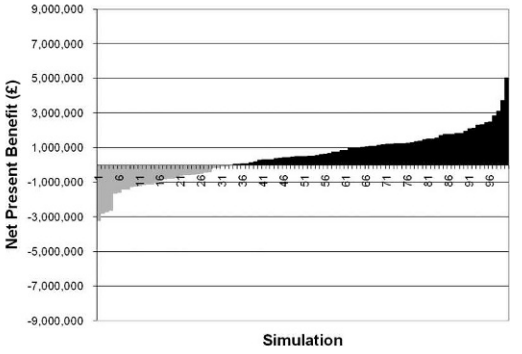

FIGURE 5. The effect of control by gas (80% efficacy) on the discounted net benefit distribution. Immigration of badgers into the control area was prevented. Each bar is the overall economic benefit of one simulation, taking into account the economics of badger control and cattle disease management.

initial decline dependent on the culling rate and a slow recovery after culling had stopped. Even though the reproductive rate was set to be density dependent (inversely proportional), because the cull area modeled was large (100 km^2 or more), the number of female badgers available to reproduce was still a limiting factor for several years after the final cull, thus preventing a rapid population recovery.

However, the numbers of infected badgers (Fig. 1), and the numbers of CHBs (Fig. 2) both showed a surprisingly large increase; in other words culling, as initially modeled, made the disease situation worse rather than better. This somewhat counterintuitive finding was a direct result of the perturbation effect, a process with an effect of much greater magnitude than the effect of varying the cull rates. This suggests that perturbation could be a more important aspect to try and influence or reduce than improving the culling rate. However, this assumes that the perturbation processes in the model are sufficiently realistic.

Given the deleterious effects of culling in our simulations, it was inevitable that the economic distributions (Fig. 3), consisted mainly of simulations that showed an overall net loss. One should be wary, though, of trying to multiply the mean simulated loss to obtain an estimate for much larger areas. Variability and uncertainty across the landscape are high, and simple extrapolation by multiplication is not justified. However, it is clear from the model results that the perturbation effects are the driving factor in determining the poor economic outcome and that if the level of perturbation is as high as in the default model, then increasing the cull rate or the area of cull or the land access compliance would not improve the likelihood of an economic benefit appreciably.

If we consider the four levels of perturbation tested in the model, the double-ring effect (the widest ranging perturbation simulated) gave the highest likelihood of economic loss. Despite being a perturbation effect of smaller "reach," changing from double-ring to single-ring did not improve the economics sufficiently, and economic loss was about as likely as economic gain. The other two possibilities of the perturbation process—the prevention of increased transmission rates and the prevention of badger immigration into the cull area—were more promising, both giving an economic benefit in about two-thirds of the simulations. However, the practicalities of achieving one of the latter two options would be very different. It does not seem possible to affect the transmission rates (i.e., to prevent an increase in transmission rates even though the badgers are perturbed). It seems more feasible to try to prevent badger immigration into the culled area, for instance by choosing an area for culling that is surrounded by a natural badger-proof border. Although it has been suggested that major roads, railway lines, and rivers could act as significant barriers to badger movements, there is some debate on what would constitute a natural badger-proof border.

This study has emphasized how important the perturbation aspect of badger culling potentially is, both in terms of TB disease control and economically. Our simulations suggest that not only is it necessary to reduce immigration when conducting badger control for TB but that it also will be necessary to determine which control methods are the cheapest and most effective. The model suggests that reality probably will lie between no chance of economic benefit and about 67% chance of economic benefit for gassing, with worse results for other methods.

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APPENDIX A—Model Variables (Temporal Settings)

Year badgers added to grid	1
Year cattle added to grid	20
First year that routine test interval switching is introduced (where parishes can change status from one test interval type to another if CHB rate low or high)	50
The algorithm[a] to determine switching is as follows:	
(1) Take the confirmed breaks in a parish over the previous 2 yr and divide by the total herds in the parish, if the percentage is greater than 1, then the testing interval is yearly (T1)	
(2) If not (1), then do as above but consider breaks over 4 yr, if the percentage is greater than 0.2, then the interval is 2 yearly (T2)	
(3) If not (2), then do as above but consider breaks over 6 yr, if the percentage is greater than 0.1, then the interval is 3 yearly (T3)	50
(4) If none of the above, then the interval is 4 yearly (T4)	
First year that premovement testing is introduced	100
Years of badger control	120–124
Years that badger perturbation is applied (cull options only)	120–127
Last year of each simulation	135

[a] This algorithm was supplied by the veterinary agency, is the one advised by the European Union, and is used in the field.

APPENDIX B—Model Variables (Spatial Settings)

	A	B	C
Target control area (km^2)	100	300	400
Grid size (squares per side)	100	160	200
Grid cell size (km)	0.2	0.2	0.2
Grid area (km^2)	400	1,024	1,600
Total parishes	30	77	120
Parishes subject to control	7	21	28
Mean parish size (km^2)	13.3	13.3	13.3
Mean control area (km^2)	93	279	373
Control area relative to grid A	1.0	3.0	4.0
Control area as proportion of simulation grid	0.23	0.27	0.23
Badger groups	300	768	1,200
Mean badger territory size (km^2)	1.33	1.33	1.33
Beef farms	70	179	280
Dairy farms	58	148	232
Mixed farms[a]	18	46	72
X4 farms[a]—mixed other species (mainly cattle)	37	95	148
X3 farms[a]	37	95	148
X2 farms[a]	37	95	148
X1 farms[a]—mixed other species (mainly others)	37	95	148
Total farms	312	799	1,248

[a] Note: Mixed farms have both dairy and beef comprising two smaller grazing areas. X1 to X4 farms represent farms that also have other stock and hence are allocated as beef or dairy, but with proportionately smaller grazing areas for cattle.

APPENDIX C—Model Variables (Badger and Cattle Parameters)

C.1. Badger Settings	
Initial badgers added per social group	
Figures obtained by iterative process to give ratio of badger ages and sexes at which the model stabilizes.	
Juvenile male	0 or 1 (mean 0.8)
Yearling male	0 or 1 (mean 0.6)
Adult male	1 or 2 (mean 1.2)
Juvenile female	0 or 1 (mean 0.9)
Yearling female	0 or 1 (mean 0.7)
Adult female	2 or 3 (mean 2.1)
Mortality rates	
Taken from fusion life tables of always healthy badgers (Wilkinson et al., 2000) at Woodchester Park. Mortality of first 2 mo from precapture mortality estimates. Mortality of 2-mo periods (including first 2 mo immediately after precapture) from life table of annual mortality: male=0.304, female=0.236. Annual mortality of superexcretors: male=0.667, female=0.480. Note: these probabilities are adjusted to be linearly inversely proportional to group size, so smaller groups have lower mortality rates. The adjustment uses a mortality rate multiplication factor based on the equation 1–{0.07[(SocialGroupAverage)–(GroupSize)]}, where SocialGroupAverage=5.7, 6.7, or 7.5 depending on whether the social group has a carrying capacity of 2, 3, or 4, respectively.	
Male first 2 mo pre-emergence	0.2400
Female first 2 mo pre-emergence	0.2400
Male not superexcretor	0.0586
Female not superexcretor	0.0439
Male superexcretor	0.1675
Female superexcretor	0.1033
Breeding probabilities	
First female	0.85
Second female [adjustable[a]]	0.40±
Third female [adjustable[a]]	0.40±
Fourth female [adjustable[a]]	0.40±
Litter size probabilities	
Taken from Neal and Cheeseman (1996, p. 160)	
1 Cub	0.08
2 Cubs	0.18
3 Cubs	0.51
4 Cubs	0.18
5 Cubs	0.05
Dispersal probabilities	
Male	0.009390
Female	0.000834
Health status transfer probabilities	
Infected to infectious	0.0309
Infected to super-	0.0274
Male infectious to infected	0.1660
Male infectious to super-	0.2511
Female infectious to infected	0.1660
Female infectious to super-	0.2511
Infection transmission probabilities	
Rates set to give a badger prevalence of ~18%, and a CHB rate of ~8%	
Infectious-badger-badger within-group	0.021000
Infectious-badger-badger between-group	0.001050

[a] Note: the probabilities of second/third/fourth female breeding are adjusted to be linearly inversely proportional to group size, so smaller groups may breed back up to size faster. The adjustment is based on the equation 0.40+([GroupSize]−6.7)× −0.079, but limited between the values 0.00 and 0.85.

APPENDIX C—Continued.

Infectious-badger-cow	0
Superinfectious-badger-badger within-group	0.042000
Superinfectious-badger-badger between-group	0.002100
Superinfectious-badger-cow	0.0005
C.2. Cattle Settings	
Farm numbers	
Calculated from June Census 2004. Farms mixed with other species (pigs, sheep, etc.) divided equally between X1 and X4. The values given below are for the 400-km^2 grid. Numbers are multiplied proportionally for larger grid sizes to maintain the right farm densities (see Appendix B).	
Total farms	312
Beef farms	70
Dairy farms	58
Mixed farms	18
X4 (mixed other sp. [mainly cattle])	37
X3 farms	37
X2	37
X1 (mixed other sp. [mainly others])	37
Grazing proportions	
Calculated from June Census 2004	
Beef farms	0.26
Dairy farms	0.46
X4	0.20
X3	0.15
X2	0.10
X1	0.05
Stocking density (beef) probabilities	
Calculated from June Census 2004 (cattle/ha)	
0.5	0.093
1.0	0.144
1.5	0.190
2.0	0.187
2.5	0.130
3.0	0.089
3.5	0.054
4.0	0.034
4.5	0.022
5.0	0.016
5.5	0.011
6.0	0.007
6.5	0.005
7.0	0.004
7.5	0.004
8.0	0.002
8.5	0.002
9.0	0.002
9.5	0.002
10.0	0.002
Stocking density (dairy) probabilities	
Calculated from June Census 2004 (cattle/ha)	
0.5	0.033
1.0	0.058
1.5	0.115
2.0	0.217
2.5	0.204
3.0	0.151
3.5	0.085

APPENDIX C—Continued.

4.0	0.051
4.5	0.028
5.0	0.019
5.5	0.011
6.0	0.010
6.5	0.004
7.0	0.003
7.5	0.001
8.0	0.003
8.5	0.003
9.0	0.000
9.5	0.003
10.0	0.001
Overstock limit	1.0
(The herd size multiplier that determines the threshold when herd size must be corrected by “selling movements”). A value of 1.0 means zero tolerance to herd size changes, and cattle are sold/bought the same time step to correct.	
Understock limit	1.0
(The herd size multiplier, which determines the threshold when herd size must be corrected by “buying movements.” A value of 1.0 means zero tolerance to herd size changes, and cattle are sold/bought the same time step to correct).	
Beef age/sex profile	
Calculated from June Census 2004	
Male 1 yr old	0.16
Male 2 yr old	0.13
Male 3 yr old	0.04
Male 4 yr old	0.00
Male 5 yr old	0.00
Female 1 yr old	0.14
Female 2 yr old	0.18
Female 3 yr old	0.20
Female 4 yr old	0.10
Female 5 yr old	0.05
Dairy age/sex profile	
Calculated from June Census 2004	
Male 1 yr old	0.07
Male 2 yr old	0.05
Male 3 yr old	0.01
Male 4 yr old	0.00
Male 5 yr old	0.00
Female 1 yr old	0.13
Female 2 yr old	0.22
Female 3 yr old	0.30
Female 4 yr old	0.15
Female 5 yr old	0.07
Cattle birthrate (per 2-mo time step)	0.159
Taken from Economics of milk production report (Coleman et al., 2004)	
Mortality rates	
Calculated from CTS slaughter data 2002–2004	
Beef male, 6 mo×1	0.0186
Beef male, 6 mo×2	0.0113
Beef male, 6 mo×3	0.0821
Beef male, 6 mo×4	0.0698
Beef male, 6 mo×5	0.3958
Beef male, 6 mo×6	0.5479

APPENDIX C—Continued.

Beef male, 6 mo×7	0.1642
Beef male, 6 mo×8	0.1796
Beef male, 6 mo×9	0.1573
Beef male, 6 mo×10	0.2028
Beef male, 6 mo×11+	0.1565
Beef female, 6 mo×1	0.0182
Beef female, 6 mo×2	0.0072
Beef female, 6 mo×3	0.0145
Beef female, 6 mo×4	0.1127
Beef female, 6 mo×5	0.3354
Beef female, 6 mo×6	0.2353
Beef female, 6 mo×7	0.1025
Beef female, 6 mo×8	0.1229
Beef female, 6 mo×9	0.1238
Beef female, 6 mo×10	0.1347
Beef female, 6 mo×11+	0.1807
Dairy male, 6 mo×1	0.1394
Dairy male, 6 mo×2	0.0180
Dairy male, 6 mo×3	0.0974
Dairy male, 6 mo×4	0.0594
Dairy male, 6 mo×5	0.3738
Dairy male, 6 mo×6	0.5367
Dairy male, 6 mo×7	0.1691
Dairy male, 6 mo×8	0.1684
Dairy male, 6 mo×9	0.1258
Dairy male, 6 mo×10	0.1616
Dairy male, 6 mo×11+	0.1484
Dairy female, 6 mo×1	0.0565
Dairy female, 6 mo×2	0.0116
Dairy female, 6 mo×3	0.0096
Dairy female, 6 mo×4	0.0303
Dairy female, 6 mo×5	0.0500
Dairy female, 6 mo×6	0.0801
Dairy female, 6 mo×7	0.0804
Dairy female, 6 mo×8	0.0910
Dairy female, 6 mo×9	0.1209
Dairy female, 6 mo×10	0.1328
dairy female, 6 mo×11+	0.1921
Bovine tuberculosis (TB) test probabilities	
Based on data analysis from T. Goodchild (UK Veterinary Laboratories Agency), giving sensitivity of 70% for standard interpretation test, 90% for severe interpretation test, and ratio of inconclusive reactors (IRs) to conclusive reactors (CRs) of 1.0 for infected cattle and 0.011 for infectious cattle.	
Based on data analysis from T. Goodchild (UK Veterinary Laboratories Agency), giving specificity of 99.7% for IRs (standard and severe test) and 99.935% (standard test) and 99.8% (severe test) for CRs.	
Based on finding that "superexcretor" cattle do not respond to the TB test (Tony Goodchild, pers. comm.).	
Standard TB test probabilities of CR	
Health category 1	0.0007
Health category 2	0.3500
Health category 3	0.6900
Health category 4	0.0007
Health category 5	0.3500
Health category 6	0.3500

APPENDIX C—Continued.

Standard TB test probabilities of IR	
Health category 1	0.0030
Health category 2	0.3500
Health category 3	0.0100
Health category 4	0.0030
Health category 5	0.3500
Health category 6	0.3500
Severe TB test probabilities of CR	
Health category 1	0.0020
Health category 2	0.4500
Health category 3	0.8900
Health category 4	0.0020
Health category 5	0.4500
Health category 6	0.4500
Severe TB test probabilities of IR	
Health category 1	0.0030
Health category 2	0.4500
Health category 3	0.0100
Health category 4	0.0030
Health category 5	0.4500
Health category 6	0.4500
TB detection probability at slaughter (of an infected animal); calculated from CTS data	0.217
Infection transmission probabilities	
Infectious and superinfectious transmission rates not differentiated for cattle. Dairy and beef are differentiated (Munroe and Dohoo, 1999)	
Dairy cow to cow within herd	0.007100
Dairy cow to cow between herds	0.000355
Superinfectious dairy cow to badger	0.000050
Beef cow to cow within herd	0.014300
Beef cow to cow between herds	0.000715
Superinfectious beef cow to badger	0.000050
Health status transfer probabilities (disease progression)	
from Fischer et al. (2005)	
Male infected to infectious	0.42
Male infected to superinfectious (anergic)	0.001
Female infected to infectious	0.42
Female infected to superinfectious (anergic)	0.001
Male infectious to infected	0
Male infectious to superinfectious (anergic)	0.001
Female infectious to infected	0
Female infectious to superinfectious (anergic)	0.001

APPENDIX D—Model Variables (Economic Parameters)
D.1. Economic Parameters and Their Values, As Used in the Fera Model.[a]

Parameter	Description	Value	Unit	Notes
Disc_rate	Discounting rate	3.5	%	Standard government rate at time of study.
SVStoDefra	SVS cost multiplier to DEFRA of TB testing costs	1.46	—	Administrative overhead multiplier.
public_share	Proportion of the costs of a CHB that are paid by DEFRA	0.4	—	
BADGER				
SetUpCost(1)	One-off set-up cost at start of control period for control by shooting	400	£/km^2	One "hunting" firearm.
SetUpCost(2)	One-off set-up cost at start of control period for control by trapping	8,675	£/km^2	Costs as for RBCT, including purchase of cage traps, vehicles, etc.
SetUpCost(3)	One-off set-up cost at start of control period for control by gassing	1,175	£/km^2	Costs as for Northern Ireland trials.
SetUpCost(4)	One-off set-up cost at start of control period for control by snaring	1,000	£/km^2	Estimate for training and equipment.
HotSpotArea	Total area of parishes categorized as type 1 or 2 for testing frequency purposes	45,177	km^2	Total area regarded as having the worst recent history of CHBs (used to scale up from model grid—area where required).
EcoMonitoringCost	Cost of survey of effects of culling on the badger and other wildlife populations	1,000	£/km^2	Cost borne by Defra and incurred at start of control and again at end of control.
IndustrySurveyCost	Cost of survey to ascertain where and how control should be done	131.92	£/km^2	Cost borne by industry, and incurred each year of control. Two 8-hr days at minimum farm labour cost of £7.67/hr (Nix, 2006) with 7.5 percent management overhead (also Nix, 2006).
CullingCost(1)	Cost of control by shooting	350	£/km^2	Estimate based on hourly wage rate. Incurred each year of control.
CullingCost(2)	Cost of control by trapping	1,387.53	£/km^2	Costs as for RBCT. Incurred each year of control.
CullingCost(3)	Cost of control by gassing	462.77	£/km^2	Costs as for Northern Ireland trials. Incurred each year of control.

APPENDIX D—Continued.

Parameter	Description	Value	Unit	Notes
CullingCost(4)	Cost of control by snaring	306.38	£/km^2	Estimate based on hourly wage plus supplies. Incurred each year of control.
DisposalCost	Cost of disposing of the carcass of each badger killed	20	£/animal	Cost borne by industry.
CATTLE				
beefSVmu	Beef slaughter value mean	7.18	—	Under log-normal scale
beefSVsd	Beef slaughter value standard deviation	0.43	—	Under log-normal scale
dairySVmu	Dairy slaughter value mean	7.28	—	Under log-normal scale
dairySVsd	Dairy slaughter value standard deviation	0.36	—	Under log-normal scale
farmCHBmu	Farm CHB cost mean	8.27	—	Under log-normal scale
farmCHBsd	Farm CHB cost standard deviation	0.99	—	Under log-normal scale
InflationBeef	Inflation of beef slaughter values	9	%	Annual Defra values, 2002–2006.
InflationDairy	Inflation of dairy slaughter values	20	%	Annual Defra values, 2002–2006.
CHBperiCattle	Cost multiplier for infected cattle being moved outside hotspot area	1.2	—	CHB per exported outbreak.
RCHBhotspot	Reactors/CHB in hotspot area	9.7	—	
RCHBreg	Reactors/CHB outside hotspot area	3.78	—	
SlaughterPerReactor	Slaughter multiplier (includes contacts)	1.18	—	Defra TB statistics
SVScostPerTest(1,1)	SVS call out cost of test	44.72	£	For small herds (≤5)
SVScostPerTest(1,2)	SVS call out cost of test	170.32	£	For large herds (≥46)
SVScostPerTest(2,1)	SVS cost of TB test	3.14	£/animal	For first 45 animals
SVScostPerTest(2,2)	SVS cost of TB test	2.016	£/animal	For animals beyond 45
VLAsampleCulturing	Veterinary Laboratories Agency culture test costs	400.53	£/CHB	
MovemtRestr(1)	Cost of beef herd movement restriction	32.7	£/farm/day	
MovemtRestr(2)	Cost of dairy herd movement restriction	6	£/farm/day	
Cval(1)	Compensation value (beef)	500	£	Per animal
Cval(2)	Compensation value (dairy)	600	£	Per animal

D.2. Farm Costs

Log-normal distributions fitted to farm survey costs for beef cattle, dairy cattle, and additional on-farm costs (Bennett and Cooke 2006).

beefSVmu=7.18	£1,313
beefSVsd=0.43	(95% probability range £555–£3,103)
dairySVmu=7.28	£1,451
dairySVsd=0.36	(95% probability range £706–£2,980)
farmCHBmu=8.27	£3,905
farmCHBsd=0.99	(95% probability range £539–£28,283)
Sensitivity tests	
SA107 (one SD high)	
beefSVmu=7.61	£2,018
beefSVsd=0.43	(95% probability range £854–£4,770)
dairySVmu=7.6	£2,080
dairySVsd=0.36	(95% probability range £1,012–£4,273)
SA108 (one SD low)	
beefSVmu=6.75	£854
beefSVsd=0.43	(95% probability range £361–£2,018)
dairySVmu=6.92	£1,012
dairySVsd=0.36	(95% probability range £493–£2,080)

[a] Food and Environment Research Agency, Sand Hutton, York, UK; CHB=cattle herd breakdown; Defra=Department for Environment, Food, and Rural Affairs; RBCT=Randomized Badger Culling Trial; SD=standard deviation; SVS=state veterinary service; TB=bovine tuberculosis.

APPENDIX E—Model Processes (Submodels)

1. Creation of badger territories

A specified number of badger territories are created: main setts are placed randomly across the grid, and grid squares are allocated to closest main sett to give fully contiguous tessellated badger groups. The grid is treated as a torus so there are no edges. The total number of badger groups added to the grid (see Appendix B) gives an average territory size of 1.33 km^2, giving a territory density of 0.75 groups/km^2.

2. Creation of Farms

A specified number of farms are added to the grid to produce a realistic density of 0.78 farms/km^2. Farm "centroids" are added to the grid at random and allocated as a farm type (beef, dairy, mixed, X1, X2, X3, X4) stochastically to give the correct proportions of farm types. X1 through X4 represent farms that also have other stock and hence are allocated as beef or dairy, but with proportionately smaller grazing areas for cattle. Potential farmland for grazing allocation is determined by tessellation from the centroids.

3. Creation of grazing areas

The grazing area for each farm is determined according to preset proportions of grazing land for each farm type (see Appendix C.2). Sufficient grid squares are marked as grazing land by using a spiraling algorithm starting from a random grid square within the farmland. Thus, all grazing area is contiguous within a farm.

4. Definition of "near farms"

The distance from each farm's grazing area centroid to every other is calculated, sorted, and stored in a matrix for later use in the "Move Cattle" procedure, so that farms buy cattle from nearby farms in preference to distant farms.

5. Creation of parishes

A specified number of parishes are created (see Appendix B) by randomly allocating grid squares as parish centroids, then tessellating around each centroid. The mean simulated parish size is 13.3 km^2.

6. Definition of neighbors

This procedure determines the badger neighbors of each badger territory, the cattle herd neighbors of cattle herds (grazing areas contiguous), and which cattle herds overlap which badger territories. This allows between-group bovine tuberculosis (TB) transmission to be simulated. Badger-to-cattle and cattle-to-badger transmission only occurs where the grazing and the badger territory overlap (as opposed to being simply adjacent).

7. Addition of badgers

Badgers are added to each badger territory at the start of year one, with some stochastic options (see Appendix C.1), to give a stable mean badger group size of about 7.5 adult badgers per group, as measured at the end of December.

8. Addition of cattle

Individual herd size is calculated from the grazing area on each farm, and a stocking density is taken at random from the stocking rate distribution (see Appendix C.2). Cattle are then added stochastically, with the use of probabilities based on the profile of ages/sexes for the herd type. For simplicity, all cattle are initially allocated to ages equivalent to the first time step of each year. Cattle are added to each farm at the start of year 1 but are kept static until year 20. The simulated stable mean herd sizes are about 44 head for beef and about 86 head for dairy.

9. Births of badgers

In the model, female badgers give birth in the first time step of each year, which is equivalent to January/February. The number of females that breed in any one badger group is determined probabilistically (see Appendix C.1), although this is limited by the number of 2+-yr-old females and the carrying capacity of the group. The breeding probability for the first female is fixed, but the probabilities of the second/third/fourth are higher for groups with fewer badgers present (linear relationship). Litter sizes are also determined probabilistically (see Appendix C.1), mean litter size is 2.94, and the cub male:female ratio is 1:1.

10. Aging of badgers

This occurs in the first time step of each year within the "Birth of Badgers" procedure. All badgers are aged by 1 yr immediately after the birth routine, but just before the new cubs are added to the main population array.

11. Mortality of badgers

Badger mortality rates (Wilkinson et al., 2000) are dependent on sex, age, and health status (see Appendix C.1) and are adjusted linearly to give lower mortality rates for smaller groups. The mortality rates are applied to individual badgers probabilistically.

12. Dispersal of badgers

Dispersal probabilities are sex dependent (see Appendix C.1) but are not related to age or season. The dispersal routine occurs every time step. Badgers disperse only as far as their neighboring group and tend to move to a group with fewer badgers if one is available. Badgers are not allowed to disperse twice in one time step.

13. Social perturbation of badgers

This procedure moves badgers to fill vacancies (see flowchart, Appendix F). It occurs whether or not badger control is being simulated, but obviously these perturbation movements are more frequent immediately after badger removal. Sexes are checked independently; groups that already have two of a sex would not receive a third, and the donor group must also have at least three more badgers of that sex than the recipient group. Badgers are moved shorter distances in preference, and a badger is not allowed to make two moves within the same time step. Note: for details of the simulated "perturbation effect," see "Transmission of TB—badger to badger" in paragraph 20 below.

14. Seeding of TB in badgers

At the start of year 20, each badger group is given a high probability of having one badger of random sex and age be infected with TB. Each selected badger during this seeding process is given a TB status of "infected."

15. Seeding of TB in cattle

At the start of year 20, about 10% of farms are chosen at random, and in each of these, a single cow of random sex and age is transferred from healthy to infected disease status.

16. Set timing for annual cattle test

At the start of year 20, each herd is allocated a random time step (between 1 and 6) to determine when it will be due for its annual TB testing program.

17. Birth of cattle

All female cattle aged over 22 mo give birth to one calf annually on their birthday. The sex ratio of the calves is set at 1:1, the sex being determined probabilistically. Over the age of 60 mo, because all cattle still alive remain in that age category, births are determined probabilistically each time step with a twice monthly birth rate. Births are applied to Main herds and Isolated herds in the same way.

18. Mortality of cattle

Mortality only applies to cattle going to slaughter. For simplicity, natural mortality on the farm is not modeled. Each cow is categorized by age into 6-mo periods, and mortality rates are applied probabilistically. The mortality rates are dependent on herd type, sex, and age but are independent of health status (see Appendix C.2). Mortality rates were calculated from the Cattle Tracing Scheme (CTS) data through construction of life tables (Appendix G). If a cow going to routine slaughter is infectious or superinfectious (not just infected), a probability of TB detection at slaughter is applied (see Appendix C.2), and if TB is detected, movement restriction and testing is triggered at the farm of origin. Mortality is applied to Main herds and Isolated herds in the same way.

19. Movement of cattle

If herd size (sum of main+any isolated herd) is smaller or larger than the ideal size (according to stocking density), extra cattle are moved on or off the farm. All spare cattle for all farms are initially moved into a holding stock (market equivalent), with males moving off a dairy farm and females off a beef farm as the priority; otherwise, cattle are picked at random (i.e., independent of age and health status). Extra animals are then chosen at random to send to "market" to ensure that 40% of cattle move each year. Cattle are then moved from "market" to farms that are short of cattle, females moving to dairy and males to beef as first priority, then proximity to donor farm as the second priority. After all within-grid movements, if more cattle are needed, they are added into the grid, and if cattle are left in the "market," they are removed to simulate movement from T1 to T3 and T4 areas. Each cow being moved into the grid is given a probability of being infectious with TB, calculated from the proportion of Britain that is T1 and from the cattle TB prevalence in the model at the time of the move. The number of infected cattle being moved outside the grid is used to calculate the extra cattle herd breakdowns (CHBs) that could be caused by those movements (e.g., from T1 to T4 areas). After year 99, if premovement testing (PrMT) is switched on, all cattle in T1 and T2 areas are tested before movement (see "Test cattle—premovement," below), and if any test from a farm is positive, movement is not allowed and standard testing procedures are triggered.

20. Transmission of TB—badger to badger

Each infectious badger has a chance of infecting every contact, both within group and between group (neighbors). Transmission rates are set higher for superinfectious badgers, and between-group rates are set to 5% of within-group rates (see Appendix C.1; Smith et al., 2001b). During years of badger control, between-group infection rates are recalculated (see "Setting transmission rates" below) to give higher TB transmission rates in and around the control area (i.e., a higher probability of between-group contacts). This is to simulate the "perturbation effect" of badger culling.

21. Transmission of TB—cattle to cattle

Each infectious cow has a chance of infecting every contact, both within-herd and between-herd (neighbors). Probabilities of transmission are currently the same for infectious and superinfectious; between herds, rates are set to 5% of within-herd rates (see Appendix C.2). Transmission rates from beef cattle are set to about twice the value of dairy cattle (Munroe and Dohoo, 1999). Unconfirmed reactors that are separated from the main herd (put together with other unconfirmed reactors in an isolated field on the farm) are classified as "isolated herds" in the model (herds isolated as part of the TB control procedures). Such isolated cattle in the model are able to transmit TB infection to each other within the isolated herd but do not transmit TB infection to any of the healthy cattle in the farm's main (nonisolated) herd or to any cattle on neighboring farms. However, it is assumed that badgers still have access to the field holding the isolated cattle, so TB transmission is still able to occur between cattle and badgers.

22. Transmission of TB—badger to cattle

Each infectious badger has a chance of infecting every contact cow that grazes on land shared by the badger (i.e., where the badger territory and the grazing land overlap). Only superinfectious badgers are given a transmission rate greater than zero (see Appendix C.1).

23. Transmission of TB—cattle to badger

Each infectious cow has a chance of infecting every contact badger where the badger territory overlaps the grazing land. Only superinfectious cows are given a transmission rate greater than zero, and it is set to the same transmission rate as from badger to cow (see Appendix C.2).

24. Setting transmission rates (including perturbation effect)

Transmission rates are applied stochastically, and default values are listed in Appendix C.1. Special rates, however, are applied to those badger groups subjected to culling and to their immediate neighbors. This is to simulate higher contact rates during a period of social perturbation as a result of the culling. This perturbation effect is simulated during the whole period of culling (5 yr) and for 3 yr after the last cull (i.e., a total of 8 yr). Wherever and whenever the perturbation effect is applied, all badger-to-badger between-group transmission rates are increased to equal the within-group rates. Badger-to-cattle, cattle-to-badger, and cattle-to-cattle rates are not adjusted.

25. Disease progression in badgers

Badgers with TB are given the chance of transferring from one TB status to another according to preset probabilities (see Appendix C.1). A badger can only make one such change per time step. Disease progression is from infected to infectious to superinfectious. Infectious badgers also have a probability of reverting back to the infected stage, but if a badger becomes superinfectious, it stays in that state until death. A newly infectious badger does not itself have the chance to infect another badger or cow until the following time step.

26. Disease progression in cattle

Cattle with TB are given the chance of transferring from one TB status to another according to preset probabilities (see Appendix C.2). Disease progression is from infected to infectious to anergic. Infected cows also have a possibility of transferring straight to the anergic state in one time step. Infectious and super-infectious cattle are not able to revert to a lower disease state, and if a cow becomes anergic, it stays in that state until death. A newly infectious cow does not itself have the chance to infect another cow or badger until the following time step.

27. Testing of Cattle

This procedure simulates both routine testing and TB-triggered testing and is recorded as a cost to government as opposed to industry. A countdown system is used to trigger the routine "whole-herd" tests for each farm at the appropriate time step, with a different countdown for "partial-herd" tests if there are isolated cattle. For the whole-herd test, both Main and Isolated cattle are tested. Every cow is tested using probabilities to determine whether it will be a Reactor or Inconclusive (see Appendix C.2). These test probabilities are dependent on cow health status and test type (standard or severe interpretation). Inconclusive (unconfirmed) reactors are modeled to simulate the processes that would occur in the field (isolation, movement restrictions, test follow-ups), including economic costs. Inconclusives are isolated, but any individuals testing Inconclusive for the third time running are classed as Reactors. Any Reactors are slaughtered and subject to postmortem examination. It is assumed that all infected reactor cows will be confirmed at postmortem, flagging a confirmed CHB and triggering movement restrictions on contiguous herds and their testing in the next time step. Test results are analyzed on a herd basis, and a herd's test status and next test requirement are stored. When a test is positive, a series of procedures are brought into effect, simulating the veterinary procedures that are used in the field. A summary of this process is described in a flowchart in Appendix H. If tests are negative, and appropriate, isolated cattle rejoin the main herd.

28. Test cattle—premovement

After PrMT has been switched on, this procedure is called whenever cattle are about to be moved, and all cattle over a specified age are tested. The costs of this testing is recorded as a cost to the farmer (Industry). Only the cattle about to be moved are tested, and in the first year of PrMT, only cattle of age 16 mo or older, and from the second year onward only cattle aged 2 mo or older. The actual values used in the field are 15 mo for the first year and 6 wk from the second year onward, but 16 mo and 2 mo were used in the model to fit in with the model's 2-mo time step. If any animals react positive to the premovement TB test, all animals of that herd are stopped from moving, and a series of procedures are brought into effect, simulating the veterinary procedures that are used in the field. A summary of this process is described in a flowchart in Appendix H. If all tests are negative, then the cattle are allowed to move (to market). Premovement testing is not applied to cattle moving straight to slaughter.

29. Aging of cattle

At every 2-mo time step, all cattle are aged by 2 mo, except those already aged to the maximum category of 30 (60 mo=5 yr), which simply stay in that category until death.

30. Switch test intervals

This procedure allows farms in a parish to switch their test interval status according to their CHB rate history. It is applied at the end of each year, from year 50 onward, and the average number of herds that have had a breakdown within the previous 6 yr is calculated for each parish. This determines what Test Interval all the farms in a parish should be (T1 to T4) (see Appendix A for details of the algorithm). In the model, a parish can only change by one category in any one year (e.g. T1 to T2, but not T1 to T3). A new test month is calculated for each farm at the end of each year, dependent on any test interval change and when the next test was due, and this new test month applies immediately.

31. Apply badger control

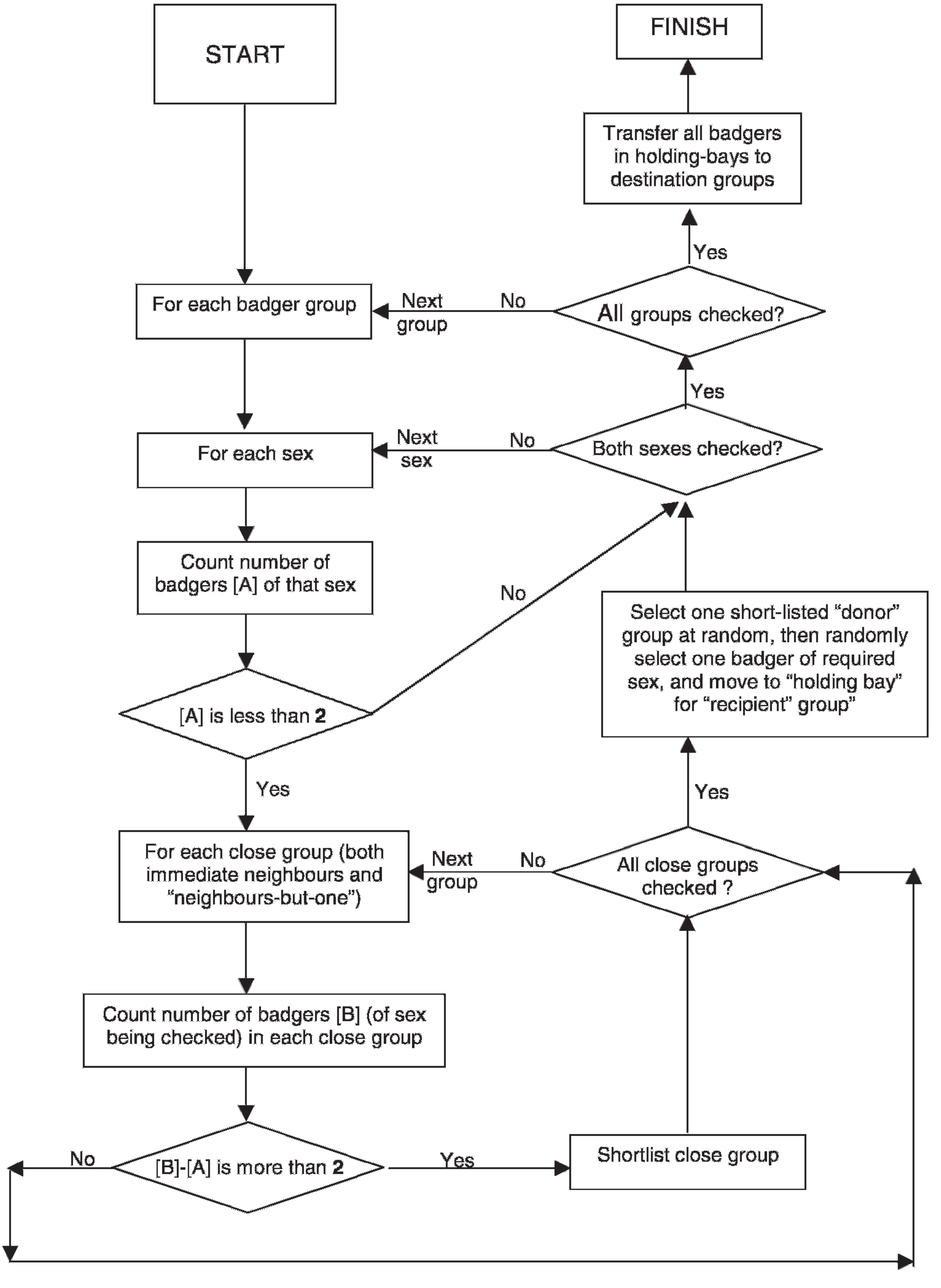
Each control method is applied for 5 yr from year 120 to year 124 inclusive, starting with identical conditions to the no-control option within that simulation at the start of year 120, to give a fair comparison between the control methods. The badger groups to be controlled are determined by selecting the parish with the highest CHB density (from years 117 to 119) and selecting the appropriate number of parishes located contiguously around it. If there are choices, the parishes with the highest CHB densities are selected. A proportion of farms are excluded at random from badger control to simulate noncompliance. If 10% or more of a badger territory overlaps with a parish selected for badger control, that badger group is marked for control. Control of the selected badger groups is applied stochastically at the specified control rate for the method every third time step (equivalent to May/June) once per year for 5 yr.

32. Save data

Output parameters are calculated at the end of each year, including badger population, badger TB (number and prevalence), CHB rates, costs of each control (Net Present Values), and control benefits compared with no control. Most outputs are summarized across the simulations, but a discounted net benefit value is output for each simulation. All output data for each set of simulations is saved in one Excel file.

APPENDIX F—Badger Movement Flowchart

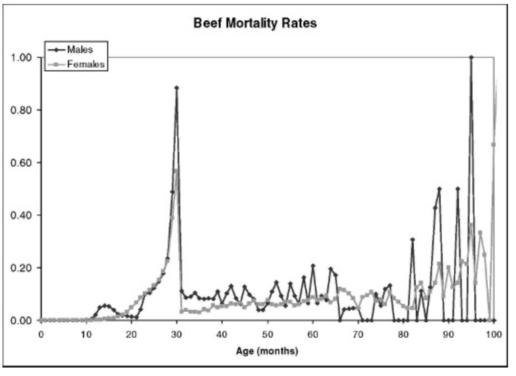
Flow-chart of simulated badger movements from populous to smaller badger groups. More movements occur after culling, as has been seen in real life.

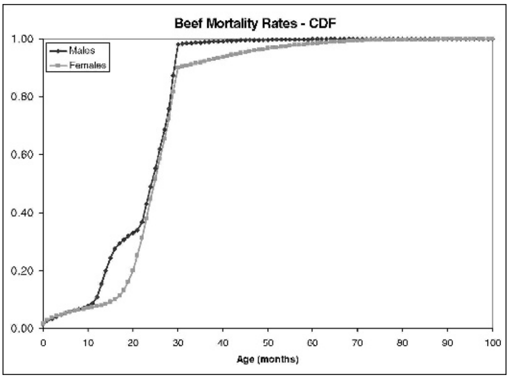


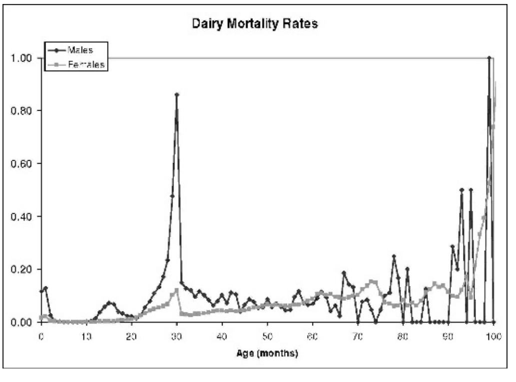
APPENDIX G—Cattle Mortality

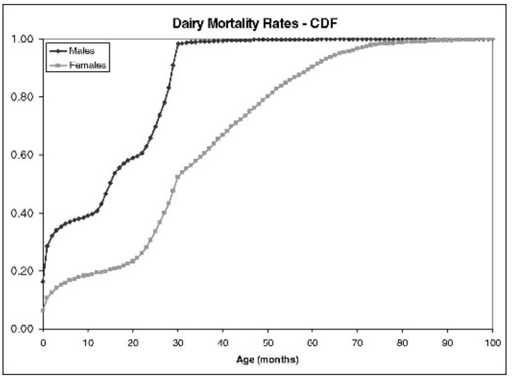
Cattle mortality (at slaughter) data, obtained from the Cattle Tracing Scheme (CTS), was plotted for beef and dairy, male and female. These are presented as monthly rates and cumulative distribution functions (CDFs).

On the basis of these results, it was decided to use a 6-mo resolution for the mortality rates (see Appendix C.2 for actual rates used). A more coarse resolution (e.g., annual) did not give realistic cattle/age distributions in the model.









APPENDIX H – CATTLE TESTING FLOWCHART