

Attempts to control tuberculosis in cattle by removing infected badgers: constraints imposed by live test sensitivity

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Summary

1. Bovine tuberculosis is a serious disease of cattle caused by the bacillus *Mycobacterium bovis*. In south-west England, badgers *Meles meles* sustain endemic *M. bovis* infection and almost certainly transmit the disease to cattle. When tuberculosis outbreaks have occurred in cattle, the Ministry of Agriculture, Fisheries and Food (MAFF) has therefore culled badgers to try to avert further outbreaks.

2. To limit the number of badgers killed, MAFF assessed a possible new strategy (the 'live test strategy') that used a serological test to identify and remove infected badgers. However, because the test correctly identified only 41% of truly infected badgers, individuals were pooled according to the setts at which they were sampled. All badgers were culled at setts where one or more seropositive animals were caught.

3. On average, 1.9 ± 1.4 (SD) badgers were sampled at each sett. Using a simple model, we show that this level of sampling still gives a low (24–37%) probability of detecting infection at a given sett.

4. Badger social groups typically occupy more than one sett. We allocated setts to social groups by using Dirichlet tessellations and field signs to predict territory borders. On average, 3.3 ± 2.8 badgers were sampled in each group. Our model shows that this increase in sample size gives probabilities of detecting *M. bovis* in truly infected groups of 43–62%, which is still likely to be unacceptably low.

5. Culling badgers according to the setts where they were trapped led to incomplete removal of social groups; some seronegative badgers were released in 61% of groups containing seropositive animals. As infection is clustered within groups, it is likely that some infected animals were released even though they tested seronegative. Incomplete removal might also cause social disruption that could accelerate the transmission of *M. bovis* between social groups.

6. We conclude that the live test strategy, as implemented, would be unlikely to reduce the overall prevalence of *M. bovis* infection in badgers, and thus the risk to cattle. Furthermore, the poor sensitivity of the serological test makes it unlikely that modifications to the live test protocol could increase its cost-effectiveness.

Key-words: bovine tuberculosis, *Meles meles*, *Mycobacterium bovis*, wildlife disease.

Journal of Applied Ecology (1999) **36**, 494–501

Introduction

Bovine tuberculosis, caused by the bacillus *Mycobacterium bovis*, is a serious disease of cattle. In Great Britain in 1996, 471 cattle herds became infected with *M. bovis*, 271 of these cases (58%) occurring in seven counties in south-west England (Cornwall, Devon, Somerset, Wiltshire, Dorset, Gloucestershire and Avon) which comprise just 10% of the land area (MAFF 1997). Regular tuberculin skin-testing of cattle, and slaughter of those animals reacting to the test, has failed to eradicate infection; this suggests that cattle are being re-infected from some outside source (Krebs *et al.* 1997). Tuberculosis is endemic in wild badger *Meles meles* L. populations in south-west England (Cheeseman, Wilesmith & Stuart 1989), and there is strong circumstantial evidence to suggest that badgers are a major source of infection for cattle (Krebs *et al.* 1997).

In south-west England, badgers live in territorial social groups (Woodroffe & Macdonald 1993). The badgers excavate complex dens (setts); each territory contains one or more main sett and a variable number of 'outlier' setts that are smaller and may be used only intermittently (Neal & Cheeseman 1996). Dispersal of individuals between social groups is rare in high-density populations (Woodroffe, Macdonald & da Silva 1995; Rogers *et al.* 1998) and transmission of *M. bovis* between groups also appears to occur infrequently (Smith *et al.* 1995). Infection within a population is usually highly localized in one or a few territories (Cheeseman *et al.* 1981, 1988).

Since 1975, the Ministry of Agriculture, Fisheries and Food (MAFF) has culled badgers in an attempt to control tuberculosis in British cattle. Following each outbreak in cattle (termed a 'herd breakdown'), epidemiological investigations have been mounted, and badgers have been culled whenever there was evidence to suggest that they were the source of infection. Between 1975 and 1997, MAFF adopted a sequence of culling strategies, although none was considered satisfactory in terms of effectiveness, cost and animal welfare (Krebs *et al.* 1997). One objection to these control strategies was that large numbers of uninfected badgers were killed, as it was only possible to identify infected animals by culture of samples collected at necropsy. For example, of the 4071 badgers culled in the years 1982–85, just 542 (13.3%) were found to be infected (Krebs *et al.* 1997). An independent review published in 1986 therefore recommended the development of a diagnostic test that could be used to identify and remove only those badgers harbouring infection (Dunnet, Jones & McInerney 1986). This test, the so-called 'live test', was based on an enzyme-linked immunosorbent assay (ELISA) and became available in 1994 (Clifton-Hadley, Sayers & Stock 1995). In the

interim period (1986–94), MAFF responded to herd breakdowns by culling badgers on land grazed by cattle that had become infected; this protocol was termed the 'interim strategy'. In 1994, MAFF devised a field trial to compare the rate of herd breakdowns around farms subject to the ongoing interim strategy with that around farms subject to a new protocol based upon the live test. This trial was halted in 1996, pending the outcome of a new independent review of policy (Krebs *et al.* 1997); this provided an opportunity to evaluate the data generated by the trial. Using these data, in this paper we show that a culling strategy based upon the live test could not have provided an effective strategy for tuberculosis control, primarily because the low sensitivity of the test and the small number of animals sampled led to a low probability of correctly identifying infected badgers or social groups.

Methods

MAFF BADGER REMOVAL OPERATIONS

All data were collected by MAFF staff and contractors in the course of implementing the live test trial (Krebs *et al.* 1997). Data were available from 23 areas in south-west England that were allocated to the live test treatment of the trial. Following each outbreak of tuberculosis in cattle, staff from the MAFF Wildlife Unit surveyed the breakdown farm and surrounding land for badgers, recording the location, size and activity of each badger sett, as well as the location of badger latrines.

Badgers' infection status was assessed during a week of live-trapping. Cage traps, baited with peanuts, were placed at each active sett. All badgers captured were anaesthetized, marked and blood-sampled; these samples were immediately subjected to ELISA testing in a mobile laboratory. The results of these tests were used to determine whether badgers should be released or killed.

Preliminary analyses (Clifton-Hadley, Sayers & Stock 1995) showed that the ELISA correctly identified only 41% of infected badgers, although 62% of badgers with tuberculous lesions, and 93% of uninfected badgers, were identified correctly. This low sensitivity meant that removing only seropositive badgers, as envisaged by Dunnet, Jones & McInerney (1986), would have involved releasing a number of truly infected badgers. To increase the chances of detecting infected animals, badgers were therefore pooled according to the setts at which they were caught. If one or more seropositive badger was caught at a sett, all animals caught there subsequently were killed, regardless of their serological status. At such setts, culling continued until there was no further sign of badger activity, usually 1–2 weeks. At setts where no seropositive badgers were

captured, all animals were released, and trapping was halted after the first week.

ALLOCATING BADGERS TO SOCIAL GROUPS

Pooling badgers according to the setts at which they were caught would increase the probability of detecting infection. However, as each social group territory usually contains several setts of various sizes (Kruuk 1978; Neal & Cheeseman 1996), culling the badgers using a particular sett might not remove entire social groups. Because *M. bovis* infection is clustered within social groups (Cheeseman *et al.* 1981, 1988), this would lead to partial removal of infection clusters, reducing the efficacy of tuberculosis control. Furthermore, as social disruption may increase the rate of dispersal between social groups, partial removal of groups might accelerate transmission of *M. bovis* among badgers (Swinton *et al.* 1997).

To measure the extent to which social groups were partially removed, we allocated setts to social group territories using the maps prepared by Wildlife Unit survey teams. These surveys did not distinguish main setts from other smaller setts. We therefore used the number of active entrances as a first stage in identifying probable main setts. The number of inactive entrances increased with the number of active entrances (polynomial regression, $F_{2,880} = 83.72$, $P < 0.0001$) but the increase was not linear ($\beta_1 = 0.76$, $t = 8.7$, $P < 0.0001$; $\beta_2 = -0.02$, $t = 3.03$, $P < 0.005$). Pairwise comparisons between setts with sequential numbers of active entrances (one vs. two, two vs. three, etc.) showed that this increase was not significant in setts with three or more active entrances (Fig. 1). This suggests some qualitative difference between setts with fewer than three active entrances and all other setts. We therefore identified setts with ≥ 3 active entrances as possible main setts, and all other setts as possible outliers. On this basis, we identified 202 possible main setts, with 12.2 ± 7.5 (SD) entrances on average (5.8 ± 3.9 active entrances and 6.4 ± 5.6 inactive entrances), and 679 outliers, with 3.2 ± 3.0 entrances on average (0.5 ± 0.7 active entrances and 2.7 ± 2.9 inactive entrances). The main setts identified by this method were spaced regularly through the landscape, suggesting that they corresponded to real main setts.

We allocated all setts to social group territories using a modification of the Dirichlet tessellation method developed by Doncaster & Woodroffe (1993). Dirichlet tessellations describe convex polygons, each containing one main sett and having the property that every point within a polygon is nearer to its own main sett than it is to any other. The tessellations are formed from segments of the perpendicular bisectors of lines joining each main sett to its

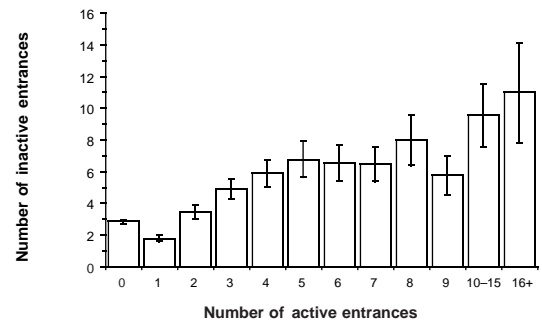


Fig. 1. Using sett size as a first stage to distinguishing main setts from other types of sett. This graph shows the relationship between the number of active and inactive entrances recorded at 881 setts (ANOVA: overall, $F_{11,869} = 19.81$, $P < 0.0001$). Pairwise comparisons between setts with sequential numbers of active holes (one vs. two, two vs. three, etc.) showed significant differences between the number of inactive entrances recorded at setts with no, one, two or three active entrances. There were, however, no significant differences in the number of inactive entrances between setts with three or more active entrances. Setts with three or more active entrances were therefore assumed to be possible main setts.

neighbours. The size and shape of each hypothetical territory is thus defined by the position of its main sett in relation to those of its neighbours. The locations of territory borders predicted by the tessellation method have been shown to give good agreement with known borders, determined by radio-tracking and bait marking, for several badger populations in Britain (Doncaster & Woodroffe 1993).

We used the tessellation method to predict territory borders at the 23 sites allocated to the live test treatment. The territory borders predicted in this way gave good correspondence with topographic features, and with the locations of latrines, which are used by badgers to mark territory borders (Fig. 2a). Tessellated borders were modified where such field signs and topographic features suggested a more probable location. In addition, 'main' setts less than 200 m apart were assumed to belong to the same social group, and their 'territories' amalgamated, unless field signs or natural boundaries indicated otherwise (in the well-studied badger population in Wytham Wood, Oxfordshire, all such paired main setts are within 200 m of one another; R. Woodroffe, unpublished data). On average, each territory contained 1.14 ± 0.36 (SD) main setts and 3.42 ± 3.35 outlier setts. We used this information to allocate captured badgers to social groups, on the basis of the setts at which they were caught.

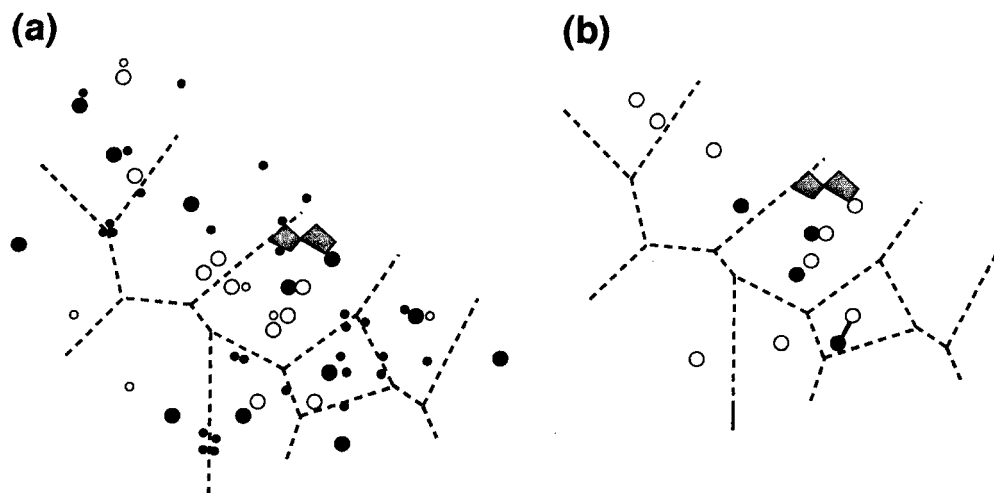


Fig. 2. Example of the process and effect of allocating setts to presumed social groups, for a single badger culling operation. (a) The use of Dirichlet tessellations to establish territory borders from data recorded on survey maps by the MAFF Wildlife Unit. Large filled circles denote setts with three or more active entrances, considered to be possible main setts; large open circles denote setts with fewer than three active entrances, assumed to be outlier setts. Small open circles are inactive setts; small filled circles are latrines. Dashed lines indicate territory borders interpolated by Dirichlet tessellations around main setts; note the coincidence between interpolated borders and the location of latrines. Shaded polygons show the fields used by cattle that reacted to the tuberculin test, prompting the badger investigation. (b) Setts at which badgers were captured during subsequent badger sampling and culling. Filled circles indicate setts where one or more badgers were found to be infected with *M. bovis* using the ELISA test; open circles show setts where none of the badgers trapped was seropositive. Note that all territories in which tuberculous badgers were caught also contained setts where all captured badgers were seronegative and were therefore released. A solid line joins two setts where badgers originally released at one sett were subsequently culled at the other.

A MODEL FOR THE NUMBER OF BADGERS
 REQUIRED TO DETECT INFECTION WITH A
 SAMPLE

As described above, the live test protocol attempted to overcome the low sensitivity of the ELISA test by pooling the badgers caught at a particular sett. To determine the extent to which this protocol improved test sensitivity, and whether pooling badgers trapped within social groups might increase sensitivity still further, we constructed a simple model to determine the probability of detecting infection when different numbers of badgers are sampled from a social group.

Let s be the sensitivity of the live test at the individual level. We define s^* as the probability that at least one animal will be identified as seropositive when badgers are sampled from the group. Comparing the values of s (individual sensitivity) and s^* (group-level sensitivity) allows us to evaluate the effectiveness of the live test protocol under different assumptions about the number of badgers caught, the true prevalence of infection, and the sensitivity of the test at the individual level. For simplicity, we assume that the ELISA test has a specificity of 100%; that is, that the test identifies all uninfected animals correctly.

The probability that there will be f truly infected badgers in a sample of g badgers (a sample preva-

lence of infection of f/g) taken from a group of n badgers where m are infected (a population prevalence of m/n) is:

$$\binom{m}{f} \binom{n-m}{g-f} / \binom{n}{g} \quad \text{eqn 1}$$

where $f \leq m$ and $g \leq n$, and where $\binom{x}{y}$ is the

binomial coefficient, defined as $\Gamma(x+1)/[\Gamma(y+1)\Gamma(x-y+1)]$ where Γ is the gamma function.

The probability that all of these f truly infected badgers give false negative results is:

$$(1-s)^f. \quad \text{eqn 2}$$

Hence s^* is 1 minus the probability that all of the badgers in the sample are classified as negative by the ELISA test, over all possible values of the number of infected badgers in the sample (up to the sample size, or the total number of infected badgers in the sett, whichever is the smaller). That is:

$$s^* = 1 - \sum_i \binom{m}{i} \binom{n-m}{g-i} (1-s)^i / \binom{n}{g}, \quad \text{eqn 3}$$

where i is 1 for the first badger sampled, 2 for the second, etc.

When only one badger is tested, equation 3 reduces to sm/n ; that is, the sensitivity at the indivi-

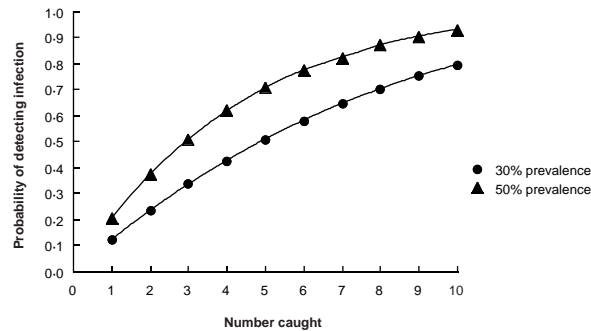


Fig. 3. Variation in the probability of detecting at least one truly infected badger, according to the number of animals sampled. This example assumes a test sensitivity of 41% at the individual level and a true prevalence of infection of 30% (e.g. three infected badgers in a group of 10; circular symbols) or 50% (e.g. five infected badgers in a group of 10; triangular symbols).

dual level multiplied by the true prevalence of infection in the group. Given a sensitivity of 41% and a true prevalence of 30%, both realistic figures (Clifton-Hadley, Sayers & Stock 1995), s^* would be only 12.3% when a single badger was caught. As more badgers are sampled, s^* increases (Fig. 3) until all the badgers in the group are caught, when equation 3 simplifies to $1 - (1 - s)^m$. For a sensitivity of 41% and when three badgers are infected in a group of 10 animals, the probability of detecting infection in the group is 79.5% if the whole group is sampled (Fig. 3).

Results

In the course of implementing the live test strategy, 483 badgers were blood-sampled at the 23 sites, of which 53 (11%) were found to be seropositive and were killed (Fig. 4a). Thirty-three (62%) of these were confirmed to be tuberculous by culture of samples taken at necropsy (Fig. 4b). A further 128 badgers were killed because they were captured at setts where seropositive badgers had been caught (Fig. 4b). Twenty-six of these had been ELISA-tested and found to be negative; four (15%) were tuberculous at necropsy (Fig. 4b). The other 102 badgers were killed without being ELISA-tested; 32 (31%) of these were culture-positive (Fig. 4b). Four hundred and four seronegative badgers were released (Fig. 4a).

Tuberculosis was confirmed by culture in a higher proportion of seropositive badgers than culled seronegative animals [62% ($n = 53$) vs. 15% ($n = 26$), $\chi^2 = 15.4$, d.f. = 1, $P < 0.0001$], although the proportion of badgers with visible tuberculous lesions was not significantly higher among seropositive animals in this sample [30% ($n = 43$) vs. 16% ($n = 19$), $\chi^2 = 1.44$, d.f. = 1, $P > 0.2$].

DISTRIBUTION OF BADGERS ACROSS SETTS

Badgers were captured at 241 setts, with an average of 1.9 ± 1.44 (SD) badgers sampled at each sett. No seropositive badgers were caught at 192 (80%) of these setts, so these badgers were released and trapping was halted.

Although our model predicts that test sensitivity should increase as more badgers are sampled, seropositive badgers were more often caught at setts where significantly fewer animals were sampled (1.45 ± 0.77 vs. 2.03 ± 1.55 badgers caught per sett; $t_{239} = 2.52$, $P < 0.05$). This difference was generated by variation between main and outlier setts in both seroprevalence and the number of badgers sampled. More badgers were sampled at main setts than at outliers (2.38 ± 1.71 vs. 1.31 ± 0.77 badgers sampled per sett; $t_{235} = 6.05$, $P < 0.0001$). However, a higher proportion was seropositive at outliers [14.8% ($n = 141$) vs. 7.8% ($n = 307$); $\chi^2 = 5.35$, d.f. = 1, $P < 0.05$].

There was no difference between main and outlier setts in either the proportion of seropositive badgers that were confirmed to be tuberculous by culture at necropsy [58% ($n = 24$) for main setts vs. 57% ($n = 21$) for outlier setts; $\chi^2 = 0.01$, d.f. = 1, $P > 0.9$] or the proportion of seropositive badgers that had visible tuberculous lesions [38% ($n = 24$) for main setts vs. 21% ($n = 19$) for outlier setts; $\chi^2 = 1.36$, d.f. = 1, $P > 0.2$]. Among badgers killed without ELISA-testing, neither the proportion of culture-positive animals nor the proportion of visibly lesioned animals was significantly higher at outlier setts [culture-positives: 28% ($n = 68$) at main setts vs. 44% ($n = 23$) at outlier setts, $\chi^2 = 1.9$, d.f. = 1, $P > 0.1$; visibly lesioned: 15% ($n = 65$) at main setts vs. 20% ($n = 20$) at outlier setts, $\chi^2 = 0.24$, d.f. = 1, $P > 0.6$].

Where badgers were sampled at both main and outlier setts within the same territory, seropreva-

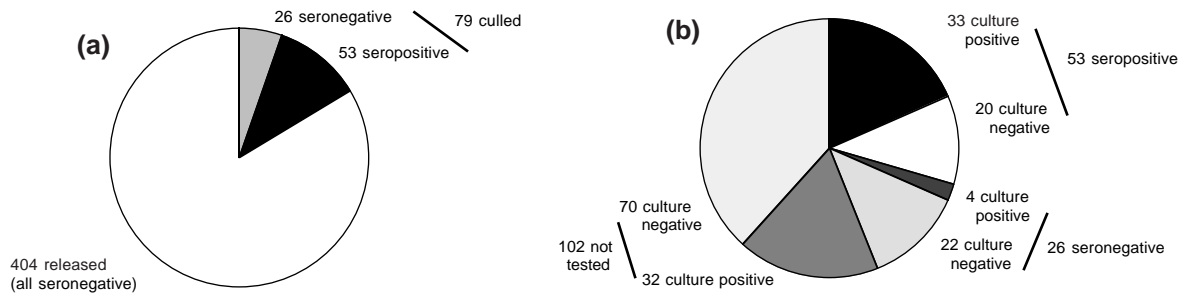


Fig. 4. Proportion of badgers showing some evidence of tuberculosis infection among (a) 483 animals that were ELISA-tested and (b) 181 animals that were culled. Twenty-six seronegative badgers, and a further 102 badgers not subjected to serological testing, were culled because they were captured at setts where one or more seropositive badgers had been caught.

Prevalence was higher at outliers (Fig. 5; Wilcoxon-matched pairs test, $T = 75.5$, $n = 12$, $P < 0.005$). This difference did not reflect any variation in body weight among badgers captured at main and outlier setts (paired $t_{11} = 0.06$, $P > 0.95$; mean weight = $9.3 \text{ kg} \pm 1.4$ at main setts vs. $9.3 \text{ kg} \pm 2.2$ at outlier setts). It was not possible to repeat these analyses using necropsy data, because there were too few territories in which badgers were culled at both main and outlier setts.

WOULD SAMPLING SOCIAL GROUPS RATHER THAN SETTS IMPROVE THE PROBABILITY OF DETECTING INFECTION?

Allocating setts to social groups increased the number of badgers sampled from 1.9 ± 1.4 (SD) per sett ($n = 258$ setts) to 3.3 ± 2.83 per social group ($n = 145$ groups). Our model predicts that doubling the number of badgers sampled from 2 to 4 should result in an increase in sensitivity from 24% to 43% if the true prevalence is 30%, or from 37% to 62% if the true prevalence is 50% (Fig. 3). By increasing the number of animals sampled, grouping setts into

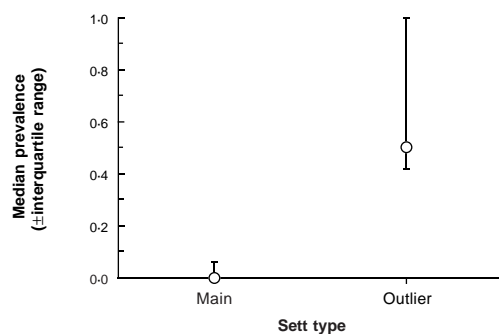


Fig. 5. Difference in prevalence recorded by ELISA testing of badgers at main and outlier setts within the same territory. Prevalence was higher at outlier setts (Wilcoxon-matched pairs test; $T = 75.5$, $n = 12$, $P < 0.005$). Data come from 12 territories sampled at seven different sites.

social groups should therefore have improved the probability of detecting infection. Nevertheless, this probability remained low in absolute terms.

WOULD ALLOCATING SETTS TO SOCIAL GROUPS IMPROVE THE EFFICIENCY OF REMOVAL?

Using the live test at the level of the sett led to partial removal of social groups (Fig. 2b). Forty-four groups contained one or more seropositive badgers; of these, 27 (61%) were only partially removed (Fig. 6). In seven of these groups, one or more animals released during the live test sampling week were subsequently caught and killed at different setts within the same territory (Fig. 2b). Of the nine animals recaptured in this way, one (11.1%) was found to be tuberculous at necropsy.

Discussion

Our results indicate that sampling and removing badgers at the level of the sett limited the effectiveness of badger removal in two ways. First, it constrained the number of badgers in each sample. On average only $1.9 (\pm 1.4)$ badgers were sampled at

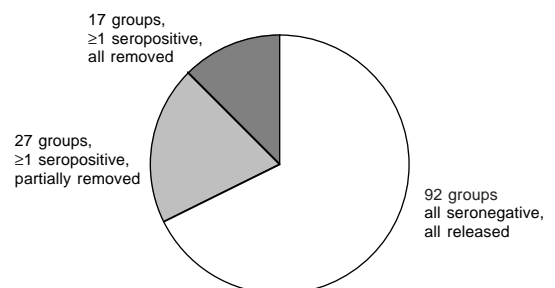


Fig. 6. The extent of badger removal in 136 badger social groups. Removing badgers according to the setts at which they were captured led to the partial removal of social groups in 17/44 (61%) territories where one or more seropositive badger was caught.

each sett. Our model shows that, even with a true prevalence as high as 50%, sampling two badgers per sett would give only a 37% chance of detecting a truly infected badger given the test sensitivity of 41%. Secondly, removing badgers according to the infection status of the other animals caught at the same sett led to incomplete removal of social groups, because each social group used 4.6 setts on average.

One way of sampling more badgers would be to extend the period during which badgers were trapped and ELISA-tested prior to removal. However, it is unlikely that this would greatly improve the efficiency of detecting infected badgers; our model indicates that doubling the number of badgers caught from 2 to 4 would still provide only a 62% probability of detecting the presence of an infected badger (assuming a true prevalence of 50%). This figure is probably still too low to form the basis of an effective tuberculosis control strategy. Pooling badgers on the basis of social group membership, rather than sett use, would also increase the number of animals sampled; while only 1.9 ± 1.4 badgers were sampled per sett, 3.3 ± 2.8 were sampled per social group. As discussed above, however, this additional sampling still fails to increase test sensitivity to levels likely to prove acceptable. Even if a whole social group of six badgers was to be sampled, the sensitivity of the ELISA test would be only 58% if two of the badgers were infected, or 78% if three were infected (Fig. 3). Thus even the highest sampling effort, sampling social groups rather than the badgers using a particular sett and sampling all the badgers in each group, could not overcome the low sensitivity of the ELISA test to give an acceptably high probability of detecting social groups containing infected badgers.

Partial removal of social groups also limited the effectiveness of the live test strategy. Sixty-one per cent of social groups that contained one or more seropositive badgers were only partially removed. In 26% (7/27) of these groups, badgers sampled and released at one sett were subsequently culled at other setts in the same territory where seropositive animals had been trapped. This demonstrates that badgers use more than one sett, so that sampling at the level of the sett fails to capture the true spatial structure of badger populations. Partial removal of social groups is likely to reduce the effectiveness of tuberculosis control in two ways. First, because tuberculosis infection is clustered within badger social groups (Cheeseman *et al.* 1981, 1988), groups where tuberculous badgers are caught are likely to contain other infected animals. Partial removal of such groups risks leaving infected animals in areas where they may transmit *M. bovis* to cattle. Secondly, anecdotal evidence suggests that disruption of social groups leads to increased movement

across territory borders (Sleeman 1992; Roper & Lüps 1993; Woodroffe, Macdonald & da Silva 1995), creating the possibility for higher rates of transmission between social groups (Rogers *et al.* 1998). Under such circumstances, partially removing badger groups might increase the prevalence of tuberculosis, exacerbating the potential risk to cattle (Swinton *et al.* 1997).

Our results show that tuberculosis prevalence, measured using the ELISA test, was higher among badgers caught at outlier setts rather than at main setts. It is possible that this difference reflected altered behaviour among infected animals; it has been suggested that tuberculous badgers may range widely and perhaps adopt a relatively solitary life-style (Cheeseman & Mallinson 1981). Alternatively, the prevalence of tuberculosis might be higher among badgers of low social status, which may spend more time in outlier rather than main setts. The difference appears to be unrelated to variation in condition or pathology among badgers caught at main and outlier setts, as badgers sampled at main setts were no heavier, and no more likely to have visible lesions, than those sampled at outliers.

In conclusion, it is unlikely that the live test trial, as implemented, would be effective in reducing the overall prevalence of tuberculosis in badgers, and hence in reducing the risk of herd breakdowns among cattle. Sampling and removing badgers on the basis of social group membership, rather than sett use, would reduce the partial removal of social groups and would result in a modest increase in sensitivity. However, this would involve more surveying and would result in the removal of many more uninfected badgers. Increasing the length of the sampling period to trap more badgers would result in a similarly modest increase in sensitivity, but at a cost of greatly increased staff resources. Even the combined use of grouping setts into social groups and sampling all members of these groups would result in poor sensitivity. Constrained by the sensitivity of the ELISA test, it is unlikely that modifications to the live test protocol could increase its cost-effectiveness. For these reasons, any future test-and-slaughter strategy for the control of tuberculosis in badgers would depend on the development of a new test with higher sensitivity.

Acknowledgements

This analysis was carried out in the course of an independent scientific review of bovine tuberculosis in cattle and badgers, commissioned and funded by the Ministry of Agriculture, Fisheries and Food. We would like to thank the other members of the review team, John Krebs, Roy Anderson, Tim Clutton-Brock, Christl Donnelly, Ivan Morrison and Douglas Young, as well as Shirley Ross, for their assistance.

Data were kindly provided by staff of the MAFF Wildlife Unit.

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Received 8 July 1998; revision received 19 March 1999