Fertility control as a means of controlling bovine tuberculosis in badger (*Meles meles*) populations in south-west England: predictions from a spatial stochastic simulation model

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SUMMARY

A spatial stochastic simulation model was used to assess the potential of fertility control, based on a yet-to-be-developed oral bait-delivered contraceptive directed at females, for the control of bovine tuberculosis in badger populations in south-west England. The contraceptive had a lifelong effect so that females rendered sterile in any particular year remained so for the rest of their lives. The efficacy of fertility control alone repeated annually for varying periods of time was compared with a single culling operation and integrated control involving an initial single cull followed by annually repeated fertility control.

With fertility control alone, in no instance was the disease eradicated completely while a viable badger population (mean group size of at least one individual) was still maintained. Near eradication of the disease (less than 1% prevalence) combined with the survival of a minimum viable badger population was only achieved under a very limited set of conditions, either with high efficiency of control (95%) over a short time period (1–3 years) or a low efficiency of control (20%) over an intermediate time period (10–20 years). Under these conditions, it took more than 20 years for the disease to decline to such low levels. A single cull of 80% efficiency succeeded in near eradication of the disease (below 1% prevalence) after a period of 6–8 years, while still maintaining a viable badger population. Integrated strategies reduced disease prevalence more rapidly and to lower levels than culling alone, although the mean badger group size following the onset of control was smaller. Under certain integrated strategies, principally where a high initial cull (80%) was followed by fertility control over a short (1–3 year) time period, the disease could be completely eradicated while a viable badger population was maintained. However, even under the most favourable conditions of integrated control, it took on average more than 12 years following the onset of control for the disease to disappear completely from the badger population.

These results show that whilst fertility control would not be a successful strategy for the control of bovine tuberculosis in badgers if used alone, it could be effective if used with culling as part of an integrated strategy. This type of integrated strategy is likely to be more effective in terms of disease eradication than a strategy employing culling alone. However, the high cost of developing a suitable fertility control agent, combined with the welfare and conservation implications, are significant factors which should be taken into account when considering its possible use as a means of controlling bovine tuberculosis in badger populations in the UK.

1. INTRODUCTION

The use of models to compare the relative efficiencies of various techniques for the control of disease in wildlife populations has become increasingly popular in recent years (Barlow 1996), and many models have compared the relative effectiveness of culling and vaccination as alternative control strategies (Barlow 1995). Growing interest in fertility control as a potential form of vertebrate population management (Hone 1992) has led to the inclusion of sterilization in analyses of possible strategies for the control of wildlife disease (e.g. Barlow 1996). One disease–host system for which it is now being considered as a possible future management option is that of badgers and bovine tuberculosis in Britain (Tuyttens *et al.* 1995). Its potential use in this disease–host system has recently been considered in an analytical mathematical manner by Swinton *et al.* (1997). The present paper complements this work by extending previous numerical simulation modelling work concerned with quantifying the relative efficiencies of culling and vaccination in the control of bovine

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tuberculosis in badgers (White & Harris 1995*a*,*b*) to a consideration of fertility control as a possible alternative management strategy.

Bovine tuberculosis (*Mycobacterium bovis*) in cattle in the UK has been largely confined to the south-west counties of Avon, Cornwall, Devon, Dorset, Gloucestershire, Somerset and Wiltshire, where badgers serve as a reservoir for the disease. Recently, there has also been an increase in the number of isolated outbreaks believed to be due to badgers outside these seven counties, particularly in Hereford, Worcester and Gwent. It is believed that excretory products from infectious badgers (urine, faeces, sputum and pus) constitute the main threat of infection to cattle (Muirhead *et al.* 1974). Since 1975, the Ministry of Agriculture, Fisheries and Food (MAFF) has undertaken badger control operations in areas where cattle have become infected with bovine tuberculosis and badgers are believed to be the most likely source of infection. These control operations have taken various forms, based initially on gassing, and later, culling following cage-trapping (White *et al.* 1993; White & Harris 1995*b*).

Up to the end of 1993, MAFF had undertaken 1096 badger control operations, all but 42 of which were in south-west England (MAFF 1994), and which involved the killing of large numbers of badgers: between 1987 and 1990, 2929 badgers were killed in 297 separate control operations (MAFF 1989, 1990, 1991, 1993). Despite this, there has been no significant decline in the incidence of bovine tuberculosis in cattle in south-west England since badger control began (MAFF 1993). Since the reactive badger-culling-based strategies used so far have failed to reduce the incidence of bovine tuberculosis, other strategies must be considered, and one possible future method being considered by MAFF is fertility control (Tuyttens *et al.* 1995; Swinton *et al.* 1997). To date, the use of fertility control has generally been restricted to small and restricted populations, and the technique has not been used to reduce population size or disease prevalence for a wide-ranging species. Furthermore, at present, there is no accepted method for the widespread contraception of badgers. Given the high expense associated with the research and development of a suitable compound, modelling provides a means of assessing in advance whether fertility control would be effective in reducing disease (cf. Barlow 1994*a*).

Previous strategies to control bovine tuberculosis in badgers have been reactive responses to the incidence of disease in cattle, and this is one factor that is likely to have contributed to their failure (White & Harris 1995*b*). The most effective means of employing fertility control would therefore be as part of a proactive strategy in those areas where the disease is endemic in badgers. Another likely reason for the failure of previous strategies is that for the culling-based strategies, lactating females have been released when captured (White & Harris 1995*b*). The extent of pseudo-vertical transmission in the epidemiology of the disease is unclear (Cheeseman *et al.* 1981, 1988; White & Harris 1995*a*), but not culling lactating females could help to maintain the infection within the population. Fertility control would avoid the need for the release of lactating females on humane grounds.

One of the required features of a compound for fertility control of badgers is that it could be successfully delivered to a high proportion of the population. Some studies have shown that effective fertility control can be achieved by the use of contraceptive implants (e.g. Bickle *et al.* 1991; Eagle *et al.* 1992). However, any method relying on surgical intervention would be impractical for a large population or over a large area. In such circumstances, an oral bait-delivered contraceptive would be much more cost-effective. For badgers, the number of cubs produced per social group is relatively constant irrespective of the number of males in a group, but is related to the number of females in their third year or older (Cresswell *et al.* 1992). For fertility control of badgers, it would therefore be most effective to concentrate on a fertility control compound that targeted females rather than males.

This paper describes the use of a spatial stochastic simulation model (developed from the one originally described in White & Harris (1995*a*,*b*)) to predict the efficacy of fertility control in controlling bovine tuberculosis infection in badgers. Fertility control was modelled as a yet-to-be-developed oral bait-delivered contraceptive directed at females. It had a lifelong effect, so that females rendered sterile in any particular year remained so for the rest of their lives. This contrasts with the fertility control modelled by Swinton *et al.* (1997) which acted for one breeding season only. Fertility control was simulated either in isolation or as part of an integrated strategy combined with culling. Integrated strategies were also compared with culling alone. Integrated strategies were investigated because under some circumstances better results will be obtained by reducing a population by more traditional methods prior to implementing fertility control (Hone 1992).

2. METHODS

(*a*) *The model*

(i) *Framework*

The basic framework of the model used in these analyses is described in full by White & Harris (1995*a*). It is a spatial stochastic simulation model that operates on a grid-cell framework. The main grid contains 100 square cells arranged in a 10×10 grid. Each grid-cell represents a territory that may contain a single group of badgers. The main grid is surrounded by a further 44 boundary cells which serve as a source of immigrants to, and a sink for emigrants from, the main grid. The disease-free equilibrium badger population density on the grid is predetermined at the social group level. It is assumed to be dependent on the availability of resources, and is the level around which density-dependent processes operate. The dynamics of group size are controlled through relations between group size, fecundity and density-dependent mortality. The transmission of *M. bovis* within and between groups occurs at pre-determined probabilities, and dispersal may also act to transmit infection between groups.

(ii) *Model structure*

The model stores information in terms of the number of constituent individuals of each sex for each of the three age

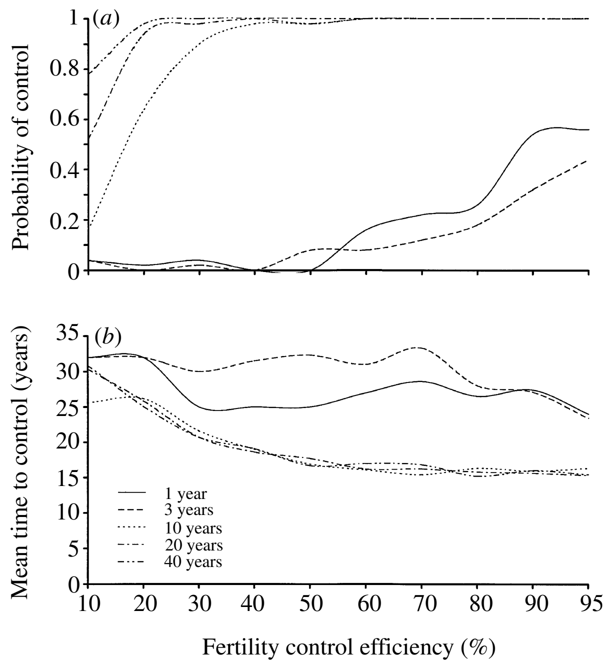

Figure 1. The effects of fertility control of varying efficiencies conducted over 1, 3, 10, 20 and 40 years' duration on (*a*) the probability of successful disease control and (*b*) the mean time taken to control disease if successful. Results are based on 50 simulations.

classes considered (adults more than two years old, yearlings 1–2 years old, and cubs less than one year old), and each disease state (susceptible, infected, and infectious). In addition, the model used for this study further subdivides adult and yearling females into (potentially) reproductively active and sterile categories.

The model runs on a quarterly basis using the following quarters: January–March (winter–spring), April–June (spring–summer), July–September (summer–autumn), and October–December (autumn–winter). These quarters were chosen to reflect changes in the behavioural patterns of badgers throughout the year (see White & Harris 1995*a*). The model consists of a main program and a series of subroutines which represent specific biological or anthropogenic processes, e.g. inter-group transmission, dispersal, disease-induced mortality, culling. These subroutines therefore constitute transitional processes, i.e. the means by which the composition of each group can be altered. In addition to the subroutines described by White & Harris (1995*a*), the version of the model used for this study incorporates a subroutine for fertility control of female badgers. This was called from the main programme for each individual adult and yearling female badger from each social group in turn if fertility control was being conducted.

Parameter values for the model were the same as those used by White & Harris (1995*a*), except for disease-induced mortality which was reduced from 63% to 48% per capita per annum, based on the more recent data of Smith *et al.* (1995). The lack of available empirical data is a major problem in calculating disease-induced mortality with any high degree of accuracy. However, this revised figure for overall disease-induced mortality for infectious animals is closer to the recent overall estimate made by Smith *et al.* (1995) for a single badger population in Gloucestershire. In four out of the six versions of the badger–bovine tuberculosis model that Smith *et al.* (1995) produced, they included an additional 'super-infectious' class to better mimic their epidemiological field data. Super-infectious animals excreted bacteria at different rates, and were subject to different disease-induced mortality compared with normally infectious animals. However, the study population modelled by Smith *et al.* (1995) is the only uncontrolled tuberculous badger population in the south-west of Britain and is atypical in terms of both the spatio-temporal stability of the disease and the exceptionally low prevalence recorded. Moreover, Smith *et al.* (1995) suggested that different badger populations may show varying resistance to bovine tuberculosis, so the introduction of two different infectious classes to a general badger population model such as the current one would be inappropriate.

(iii) *Badger group size*

White & Harris (1995*a*) quantified the effects of group size on the potential rate of spread of bovine tuberculosis. Their model showed that there was a theoretical threshold disease-free equilibrium group size below which bovine tuberculosis was unlikely to spread and could not become endemic. Under normal circumstances of movement and inter-group contact, this was around six adults and yearlings. Although the disease would persist at this density for long periods of time, it was always in decline. In contrast, at a mean disease-free equilibrium group size of eight adults and yearlings, the probability of disease spread and persistence was much increased and the disease could become endemic. This finding is also supported by more recent work (Smith *et al.* 1995). Since the aim of this study was to assess the impact of varying levels of fertility control in an endemic disease situation, a disease-free equilibrium group size of eight adults and yearlings was used in the model.

(iv) *Inter- and intra-group infection probabilities*

White & Harris (1995*a*) showed that a variety of combinations of inter- and intra-group infection probabilities could replicate the observed patterns of spread and prevalence of bovine tuberculosis. However, the highest mean prevalence at apparent equilibrium and the most rapid spread of infection from a point source were obtained with a combination of an intra-group infection probability of 0.05 and an inter-group infection probability of 0.01. These specific values were also used by White & Harris (1995*b*) to assess the efficacy of various past and present control strategies for the control of the disease, so they were used in this study as well for consistency and to ease comparison of results.

(v) *Pattern of initial infection*

Since the aim in this study was to replicate an endemic infection within the badger population, the infection was initially introduced into all groups on the grid in the form of one infected male in each group. This pattern of initial infection will never be seen in the field, but is an approximation to the initial widespread exposure of the badger population to infection from cattle (White & Harris 1995*a*). It resulted in an apparent equilibrium disease prevalence being reached after approximately 60 years, at which stage it exhibited a clumped distribution in the badger population similar to that observed in the wild. Since the aim of this study was to investigate the effect of fertility control on endemic disease, fertility control was never started until year 60 when a pattern representative of endemic disease would have become established.

(*b*) *Fertility control*

The efficiencies of fertility control (the proportion of adult and yearling females reached and rendered infertile by the oral bait-delivered contraceptive) used for the study ranged between 10% and 95%. Fertility control took place in the spring–summer quarter (April–June) of each year. For a particular control efficiency, each individual adult and yearling female badger was independently subjected to the specific equivalent probability of being reached by the contraceptive and rendered infertile. Thus, for a 60% efficiency of fertility control, each badger was subjected to fertility control independently with a probability of 0.60. Annually repeated fertility control was simulated for periods of 1, 3, 10, 20 and 40 years. Fifty simulations were run for each set of conditions.

(*c*) *Integrated control*

White & Harris (1995*b*) showed that single culling operations of less than 60% efficiency were ineffective in controlling endemic bovine tuberculosis in badger populations, but that above this efficiency, the probability of successful disease control increased markedly. Maximum efficiency of badger control during the two culling-based strategies in which badgers were trapped around the setts was 70–80% (White & Harris 1995*b*). Since this is the form of control adopted under the current control strategy, two different culling efficiencies, 60% and 80%, were used for this analysis. As with fertility control, for a particular culling efficiency each individual badger was independently subjected to the specific equivalent probability of being culled, and culling took place in the spring–summer quarter (April–June) of each year. For integrated control, culling took place in the first year, and annually repeated fertility control took place for periods of 1, 3, 10, 20 and 40 years, starting at the same time as the onset of culling. Thus in the first year of any integrated control strategy, the badger population was subjected to both culling and fertility control. A culling-only strategy was also simulated to act as a control for comparisons of efficacy between different strategies. Fifty simulations were run for each set of conditions.

3. RESULTS

(*a*) *Fertility control*

(i) *Probability and time taken for successful disease control*

The probability of successful disease control and the mean time taken to control endemic disease if successful following fertility control operations of varying efficiency and duration are shown in figure 1. The probability of successful disease control was greater, and the mean time taken to successful control less, for increased efficiencies of fertility control conducted over longer periods of time. The probability of successful disease control for control periods of 10, 20 and 40 years was markedly greater than for periods of one and three years.

(ii) *Effect on disease prevalence and badger density*

The effect of various durations of fertility control on the prevalence of bovine tuberculosis and mean badger group size is shown in figure 2. The effects of 1-, 3- and 10-year fertility control only are shown. In every case disease prevalence was reduced. However, when fertility control was employed for a duration of three years or less, less than 1% prevalence was only achieved when high fertility control efficiencies (90–95%) were used. When fertility control was employed for ten years, the disease declined to less than 1% prevalence over a wider range of efficiencies (20–95%). The effects of 20- and 40-year fertility control were very similar to ten-year fertility control in terms of their effects on disease prevalence, although the disease was also reduced to less than 1% prevalence by 10% control efficiency over these longer periods of time.

The badger population did not appear to be able to recover once the mean group size had fallen below about one individual. Although it could still persist for some time at such low mean group sizes, this level was therefore taken as the minimum population density required for the badger population to remain viable over the long-term. For fertility control lasting one and three years, the badger population remained viable and showed signs of recovery at all efficiencies of fertility control. For control lasting ten years, this was only the case for efficiencies below 40%. For control of 20 years' duration, the badger population showed some signs of recovery after 20% control efficiency, but not after 40% control efficiency. For 40-year fertility control, the badger population remained in decline throughout the period of the simulations for all fertility control efficiencies. The mean prevalence of the disease did not decline to zero while a viable badger population was maintained under any of the conditions tested. Only under certain restricted conditions did fertility control result in disease prevalence being reduced to below 1% while a viable badger population was still maintained (table 1).

(*b*) *Integrated control*

(i) *Probability and time taken for successful disease control*

The probability of successful disease control and the mean time taken to control endemic disease if successful following integrated control are shown in figure 3 for an initial cull of 60% and figure 4 for an initial cull of 80%. The probability of successful control was close to 1.0 under most of the conditions tested, except for when a 60% cull was followed by one-year fertility control at efficiencies less than 70%, and three years' fertility control at efficiencies of less than 40%. In general, the mean time taken to successful disease control decreased with increased culling efficiency, increased levels of fertility control, and increased duration of control.

(ii) *Effect on disease prevalence and badger density*

The effect of a single cull at efficiencies of 60% and 80% on disease prevalence and mean badger group size is shown in figure 5. For both culling efficiencies, the effect of the initial cull was to bring the prevalence of disease down to a lower level than was achieved by fertility control alone. For single 60% and 80% culls, disease prevalence was reduced to less than 2% and less than 1%, respectively, after 6–8 years following control, and in most instances a viable badger population was maintained. However, neither efficiency of culling resulted in the eradication of disease when used alone rather than as part of an integrated strategy.

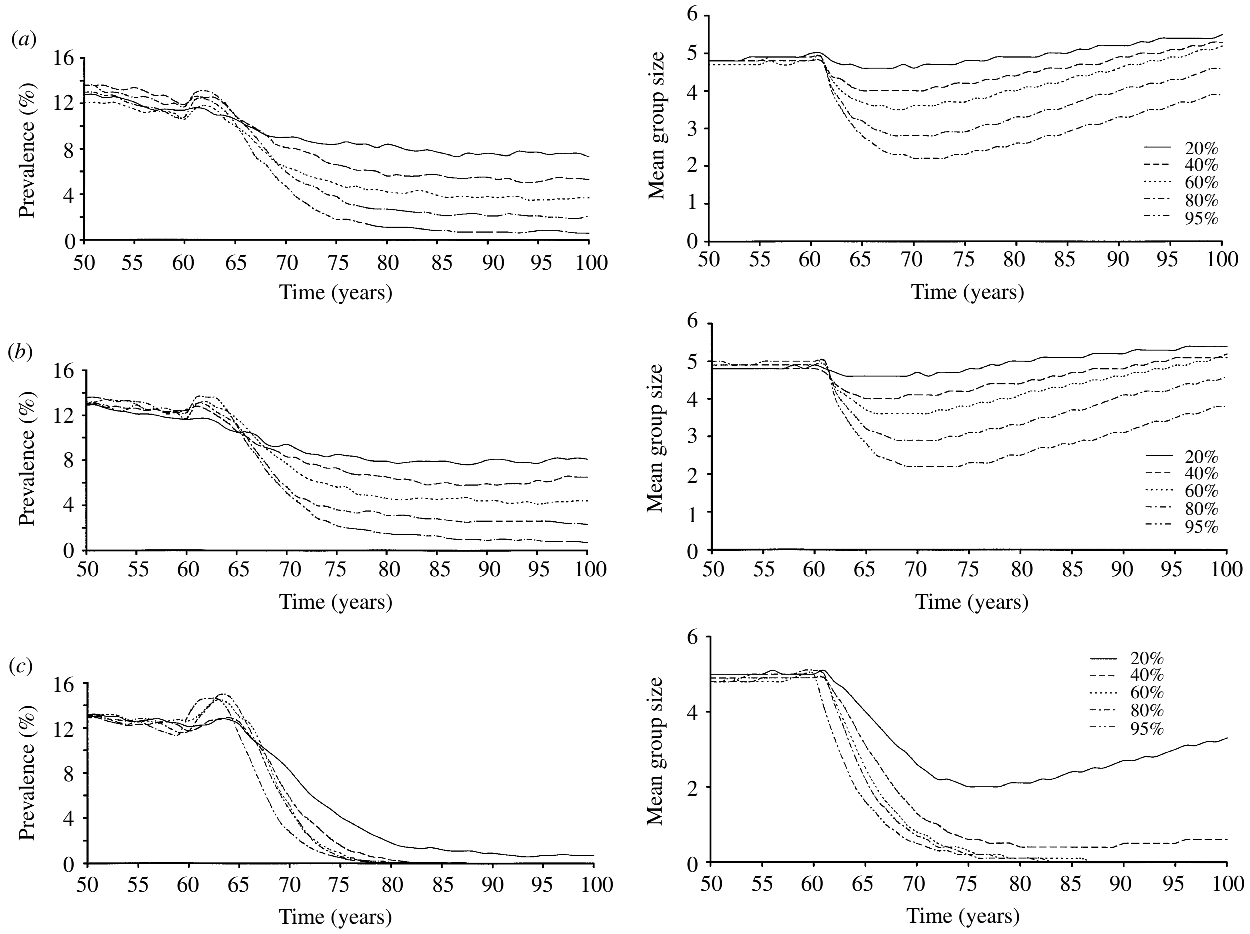

Figure 2. The effects of fertility control of varying efficiencies and durations on disease prevalence and mean badger group size over time following the onset of control in year 60 for ferility control of (*a*) 1 year (*b*) 3 years' and (*c*) 10 years' duration. For clarity, only fertility control efficiencies of 20%, 40%, 60%, 80% and 95% are shown. Results are means based on 50 simulations.

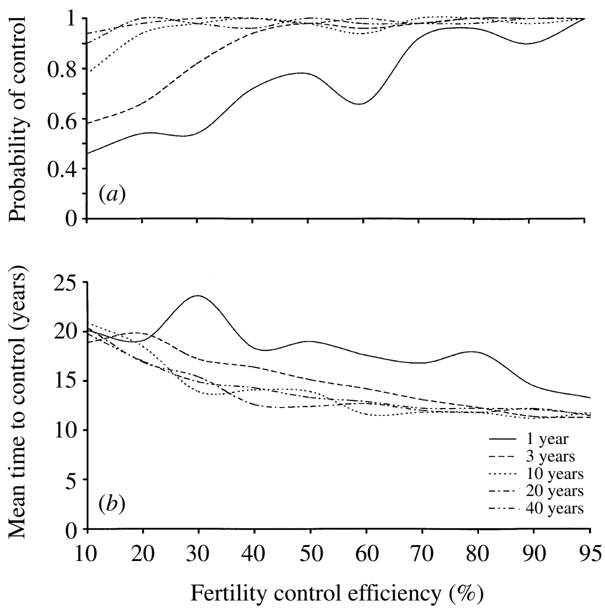

Figure 3. The effects of integrated control combining an initial 60% single cull with fertility control of varying efficiencies conducted over 1, 3, 10, 20 and 40 years' duration on (*a*) the probability of successful disease control and (*b*) the mean time taken to control disease if successful. Results are based on 50 simulations.

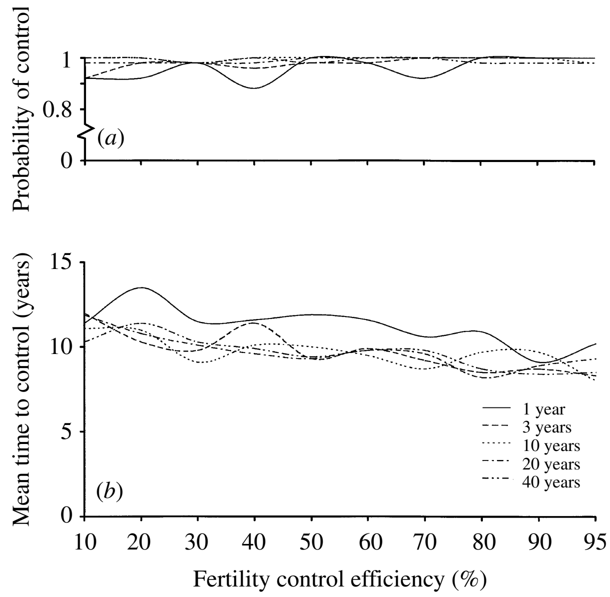

Figure 4. The effects of integrated control combining an initial 80% single cull with fertility control of varying efficiencies conducted over 1, 3, 10, 20 and 40 years on (*a*) the probability of successful disease control and (*b*) the mean time taken to control disease if successful. Results are based on 50 simulations.

Table 1. *Conditions of annually repeated fertility control of different durations under which the mean prevalence of the disease declined to below 1%, and a viable badger population was maintained*

(Results are based on 50 simulations.)

duration of fertility control (years)	fertility control efficiency (%)	eradication of disease	number of years for disease to decline to <1% prevalence	mean number of badgers per group at year 100
1	95	no	24	3.9
3	95	no	30	3.8
10	20	no	29	3.3
20	20	no	22	1.2

Table 2. *Conditions of culling alone and integrated control, incorporating a single culling operation and annually repeated fertility control of different durations, under which the mean prevalence of the disease declined to* <1% *and a viable badger population was maintained, for single initial culls of* (*a*) 60% *and* (*b*) 80% *efficiency*

(Results are based on 50 simulations.)

	duration of fertility control (years)	fertility control efficiency (%)	eradication of disease	number of years for disease to decline to <1% prevalence	mean number of badgers per group at year 100
(*a*)	1	40	no	17	4.5
	1	60	no	14	3.8
	1	80	yes	12	3.1
	1	95	yes	10	2.2
	3	20	no	16	4.5
	3	40	yes	11	3.0
	3	60	yes	10	1.7
	10	20	yes	14	2.2
(*b*)	0	–	no	6	4.0
	1	20	yes	7	3.7
	1	40	yes	6	3.1
	1	60	yes	7	2.7
	1	80	yes	7	1.8
	1	95	yes	7	1.2
	3	20	yes	7	2.9
	3	40	yes	8	1.9
	3	60	yes	8	1.0
	10	20	yes	8	1.2

The effect of integrated control employing single culls followed by fertility control of varying efficiencies and durations is shown in figures 6 and 7 for culling efficiencies of 60% and 80%, respectively. The effects of integrated control employing 1-, 3- and 10-year fertility control only are shown. Integrated strategies employing both culling and fertility control caused disease prevalence to decline to lower levels than when culling alone was used, although the mean badger group size was also reduced. An integrated strategy employing an 80% initial cull reduced bovine tuberculosis prevalence to lower levels in a shorter period of time than an integrated strategy with a 60% initial cull, and resulted in a greater reduction in the badger population. In general, there were about 1.5 less badgers per group following an integrated strategy with an 80% initial cull compared with a 60% initial cull. The effects of integrated control employing 20- and 40-year fertility control were very similar to integrated control employing 10-year fertility control at all fertility control efficiencies in terms of their effects on disease prevalence. However, they showed some differences in terms of their effects on mean badger group size for the lower fertility control efficiencies of 20% and 40%. For integrated control combining a 60% or 80% initial cull with 20-year fertility control, the badger population persisted after 20% fertility control, but not after 40% fertility control, and for integrated control combining a 60% or 80% initial cull with 40-year fertility control, the badger population did not persist at either 20% or 40% fertility control efficiencies. Only under certain restricted conditions did integrated control result in disease prevalence being reduced to zero prevalence or less than 1% while a viable badger population was still maintained (table 2).

4. DISCUSSION

One of the problems with culling as a management strategy for the control of wildlife disease in territorial group-living animals such as badgers is that the

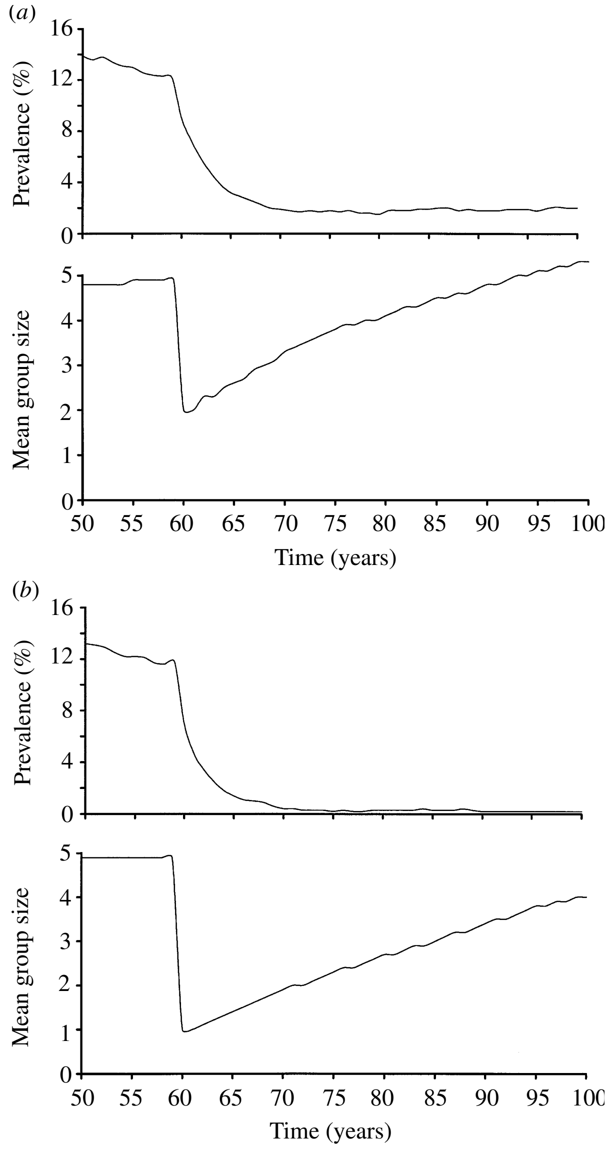

Figure 5. The effects of single culling operations of (*a*) 60% and (*b*) 80% efficiency on disease prevalence and mean badger group size over time following control in year 60. Results are means based on 50 simulations.

removal of social groups causes increased inter-group movement (Cheeseman *et al.* 1988). This results in an increase in the frequency of aggressive social contacts, which increases the probability and rate of spread of bovine tuberculosis in the badger population (Brown *et al.* 1994; White & Harris 1995*b*), and lowers the threshold population density required for the disease to persist. One of the arguments favoured by proponents of fertility control is that it could avoid these problems. For this reason fertility control may constitute a more humane and therefore ethically acceptable method of wildlife population control (Tyndale-Biscoe 1991). Furthermore, when problems of culling-based perturbation are taken into account, the relative efficacies of culling-based control compared with fertility control for group-living animals such as badgers may be less clear (Swinton *et al.* 1997).

However, there are also many potential problems associated with fertility control, from both a practical disease control perspective and an animal welfare one. Decreasing the population density locally by fertility control could result in a breakdown of the existing territorial system, and consequently a greater frequency of social contacts and hence disease spread, in much the same way as with culling. There are further associated welfare problems. For a significant proportion of the year, the activities of breeding animals are focused around their young, and if this focus is removed, the quality of life of these individuals will be adversely affected. Furthermore, sterilizing animals causes them to live longer. This has two effects. First, animals that live longer tend to develop a number of problems typical of senescence that they would not normally experience. Secondly, increasing longevity offsets the benefits of fertility control to some extent. This would be of particular significance for badgers and bovine tuberculosis due to both the longevity of badgers under normal circumstances and the chronic nature of the disease.

There are many unknown factors associated with the practical use of fertility control as a management strategy for group-living animals, and these will depend to a large extent on the reproductive biology of the species concerned. From a study of badgers in south-west England over the period 1988–1990, Cresswell *et al.* (1992) found that only 44% of adult females produced cubs each year; 9% did not ovulate, 13% ovulated but were not fertilized, and 34% were fertilized but failed to implant their blastocysts. Furthermore, of those that produced cubs, 35% ceased to lactate before the cubs could have been weaned, so less than 30% of the total potential productivity was achieved. A separate study conducted over an earlier time period (1973–1980) found that only 11% of total potential productivity was achieved (Page *et al.* 1994). From these studies, it is clear that badger populations are breeding at well below their maximum reproductive potential. The efficacy of a fertility control strategy for badgers would therefore be dependent on the responses of the various reproductive classes of females. It is unlikely that those that do not normally become pregnant would become pregnant whatever the situation. The main interest concerns those females that produce litters but fail to raise them successfully and those that are fertilized but fail to implant their blastocysts. If the dominant sows were removed, some of the former non-breeders would assume dominant status and therefore be likely to raise their litters successfully. This in-built ability for compensation in fecundity may therefore offset the initial effects of fertility control in reducing badger population density.

The results of any modelling exercise such as this need to be interpreted with caution, since they represent an idealized theoretical world rather than the full complexities of reality. In circumstances such as those addressed by this study, where real field data against which to test the predictions are not available, even greater care is needed since any predictions can not be validated. However, spatial stochastic models of disease such as this one offer a closer representation of reality than non-spatial deterministic ones, especially where the host population displays marked spatial

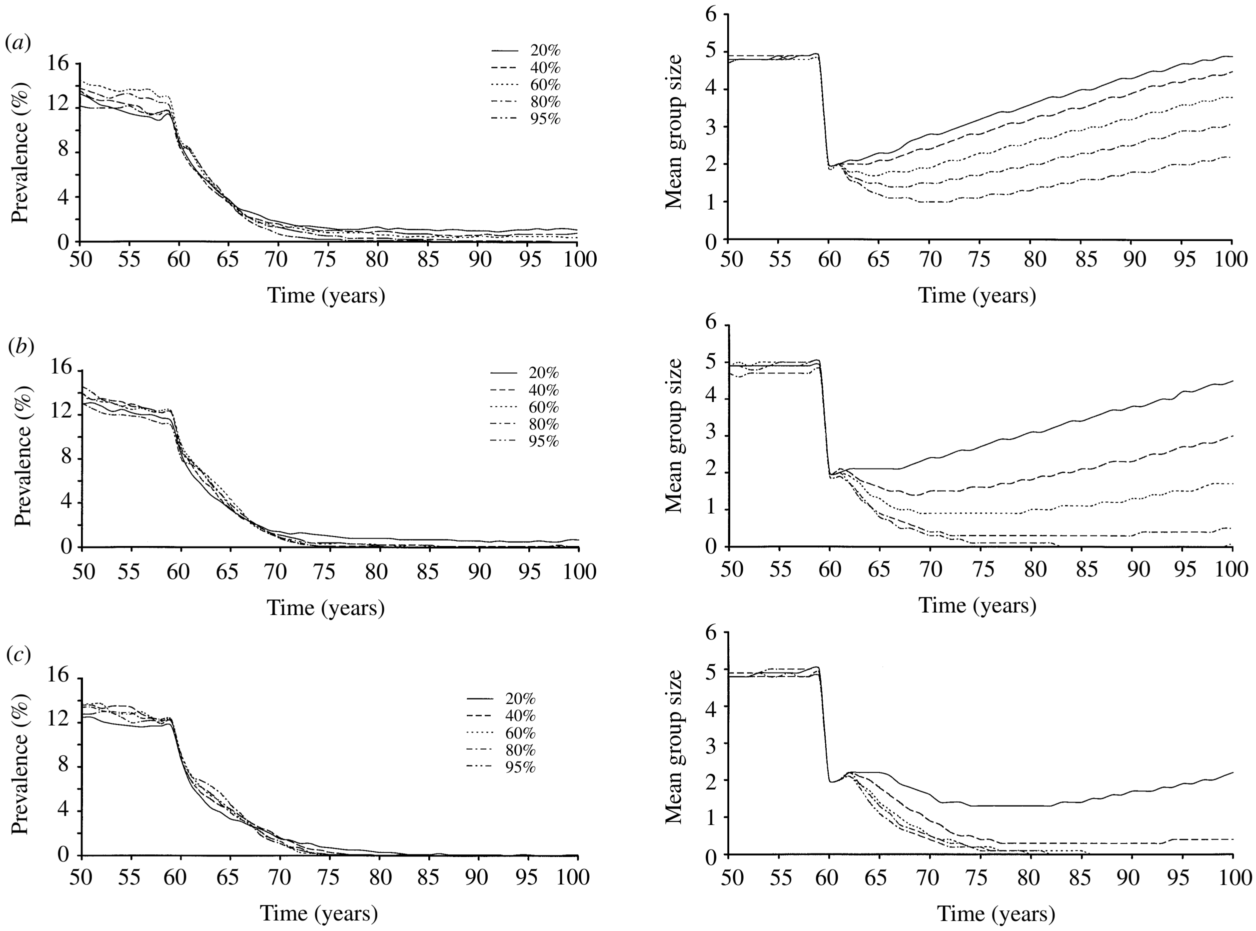

Figure 6. The effects of integrated control incorporating an initial 60% cull followed by fertility control of varying efficiencies and durations on disease prevalence and mean badger group size over time following the onset of control in year 60 for fertility control of (*a*) 1 year, (*b*) 3 years' and (*c*) 10 years' duration. For clarity, only fertility control efficiencies of 20%, 40%, 60%, 80% and 95% are shown. Results are means based on 50 simulations.

organization, as is the case for badgers (White & Harris 1995*a*). Moreover, earlier versions of this model have been used successfully to mimic the prevalence and distribution of endemic bovine tuberculosis in badger populations, as well as the relative efficacies of different control strategies, and these results have been supported by field data where available (White & Harris 1995*a*,*b*), as well as by subsequent, independent modelling work (Smith *et al.* 1995).

The discussion above has indicated the many problems associated with the use of modelling to evaluate a yet-to-be-developed fertility control strategy. However, because of the large number of unknowns concerning behavioural factors such as dominance hierarchies, territoriality, social interactions and social suppression of reproduction, they have been ignored in the modelling component of this study. Thus, in the model, fertility control has no adverse implications for the social organization of the population, and productivity of the badger populations is solely related to the number of adult females in the group (White & Harris 1995*a*) rather than mediated through social and behavioural factors.

Under no conditions tested by this modelling exercise did a strategy of fertility control alone result in the eradication of the disease while a viable badger population was still maintained. Fertility control with an efficiency of 20% employed annually over a 10 or 20 year period reduced disease prevalence to below 1% within 30 years, and following 10-year fertility control, an average of more than three badgers per group remained at year 100. However, for this duration of control, any higher efficiency of fertility control resulted in the badger population being reduced to non-viable levels. There were only two sets of conditions where fertility control alone conducted over shorter periods of time had an equivalent efficacy. These were for periods of one or three years with a fertility control efficiency of 95%. Even under these conditions, it took 24–30 years for the disease to reach less than 1% prevalence. Moreover, it would be extremely difficult to achieve such high levels of fertility control in practice.

Where fertility control was used as part of integrated control strategies, disease prevalence was reduced more rapidly and to lower levels than fertility control alone. Under certain integrated control strategies, bovine tuberculosis could be eradicated completely while will maintaining a viable badger population, although this only occurred under a limited set of conditions, most frequently where a high level cull (80%) was followed by a low to intermediate level of fertility control (20–60%) over a short to moderate time period (110

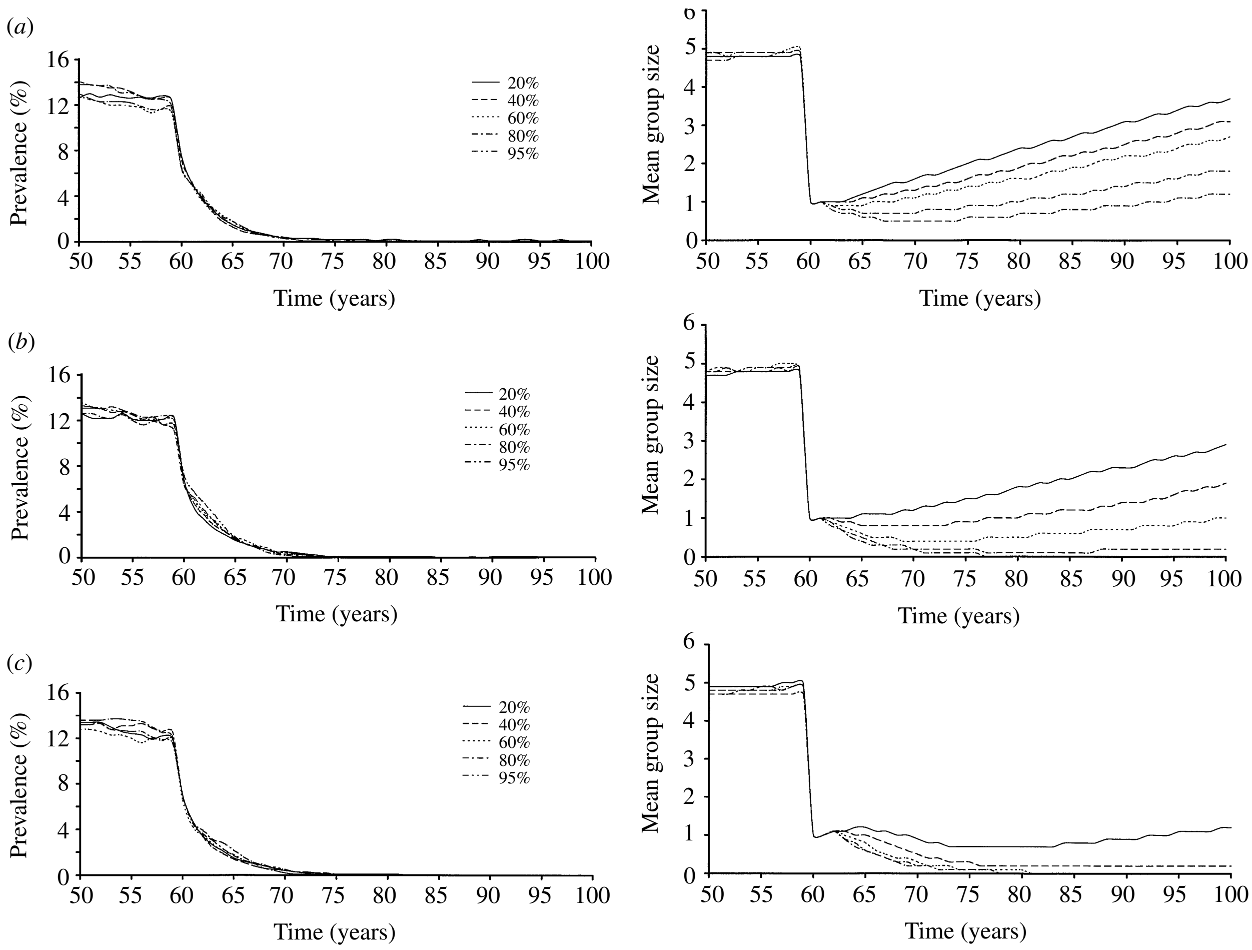

Figure 7. The effects of integrated control incorporating an initial 80% cull followed by fertility control of varying efficiencies and durations on disease prevalence and mean badger group size over time following the onset of control in year 60 for fertility control of (*a*) 1 year, (*b*) 3 years' and (*c*) 10 years' duration. For clarity, only fertility control efficiencies of 20%, 40%, 60%, 80% and 95% are shown. Results are means based on 50 simulations.

years). Lower fertility control levels allowed the badger population to regenerate more rapidly in compensation for the population reduction following the initial cull (more cubs are born and subsequently survive), and the reduced incidence of disease resulted in lower levels of disease-induced mortality. However, as the duration and efficiency of fertility control increased, the mean badger group size at the end of the 100-year simulation period was reduced. For a 60% initial cull, this was compensated for by a reduction in the time taken to reduce disease prevalence, but for an 80% cull, the efficiency of fertility control had little effect on the time taken to reduce disease prevalence.

The results of this study show that for fertility control based on an oral bait-delivered contraceptive to be effective in controlling bovine tuberculosis in badgers, it would have to be employed as part of an integrated strategy. However, for an integrated strategy, there was only a relatively limited range of culling and fertility control efficiencies over which successful disease control could be effected while maintaining a viable badger population, and even under the most effective integrated strategies, it took more than 12 years for the disease to be completely eradicated from the badger population.

The optimum strategy for a control programme for bovine tuberculosis in badgers may therefore be not to attempt to eradicate the disease completely, but rather to reduce it as quickly as possible to very low levels at which the risk to cattle would be minimal. The results of this modelling study suggest that the most effective approach involving fertility control would be to combine an initial 80% cull with 1–3 years of fertility control reaching 20–40% of the female population. Although it would take more than 12 years for the disease to be eradicated, disease prevalence would fall to below 1% within 6–8 years after the onset of control.

For some severe wildlife management problems in other countries attention is being focused on immunocontraception. For example, for the control of brushtailed possums (*Trichosurus vulpecula*) in New Zealand, which are the main wildlife reservoir for bovine tuberculosis in that country and also pose a serious threat to large areas of native broadleaf/podocarp forests (Green 1984; Batchelor & Cowan 1988), the use of a microbial vector which carries an immunocontraceptive antigen is being considered. A sexually transmitted herpes-type virus is being given specific attention as this carries with it several advantages, such as its success being independent of density (Barlow 1994*a*,*b*). The fundamental problem of immunocontraception is irreversibility, and an efficient immunocontraceptive would be out of the control of wildlife managers as soon as it was released into the population (Tyndale-Biscoe 1994). For the British badger population, because of its conservation importance (Harris *et al.* 1995), such a risk would be unacceptable.

In the meantime, other options for controlling bovine tuberculosis must be considered. At present, a vaccine for badgers is undergoing trials in Ireland (Stanford *et al.* 1993), but nothing has been published regarding its degree of success. White & Harris (1995*b*) used modelling to show that repeated vaccination directed proactively in those areas with a history of bovine tuberculosis infection in badgers would be the most effective strategy for the long-term eradication of the disease from badgers in south-west England, and this is also supported by the views of other authors (Morris & Pfeiffer 1991; Stanford *et al.* 1993). However, the development of a suitable vaccine for badgers is a long way off, and solutions to the bovine tuberculosis problem need to be found urgently.

Despite 25 years of badger control, bovine tuberculosis in cattle is increasing. The reactive culling-based strategies used to date have failed to control the disease, and the present study has shown that fertility control of badgers would be ineffective unless used as part of an integrated control strategy. The question remains as to whether an integrated strategy would offer significant advantages over a single high-efficiency cull directed proactively. While the incorporation of fertility control within an integrated strategy did increase the rate of decline of disease, the differences were minor and were only apparent once the disease had already reached very low (less than 1%) prevalence. The use of a single 80% cull alone reduced the disease prevalence to below 1% after 6–8 years, and in addition, the recovery of the badger population was more rapid compared with an integrated strategy with the disease remaining at a low level. A culling-only strategy directed proactively could therefore reduce the risks of transmission of the disease to cattle substantially and be a major benefit to the farming community.

The most important difference between the culling-based and integrated control strategies for the control of bovine tuberculosis in badgers modelled in this paper is that the integrated strategies were able to eradicate the disease entirely from the badgers while still maintaining a viable badger population, whereas the culling-based strategies could only reduce the disease to very low levels under the same conditions. However, when considering the dynamics and control of bovine tuberculosis in badgers, it is important not to be distracted from the real problem, which is the occurrence of the disease in cattle. The key policy research questions that emerge from this work regarding the potential use of fertility control in badgers for the control of bovine tuberculosis in cattle are, therefore, whether (i) the gains in control of tuberculosis in badgers resulting from the use of an integrated control strategy compared with a culling-based one would result in a significant reduction in the risk to cattle, and (ii) whether the benefits of this reduced risk to cattle would be likely to exceed the costs incurred in the search for and development of an appropriate fertility control agent for badgers. Moreover, the costs and benefits considered in addressing these questions should not be confined to financial ones, but should also incorporate an appreciation of the welfare and conservation issues relevant to the badger population.

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