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Culling-induced social perturbation in Eurasian badgers *Meles meles* and the management of TB in cattle: an analysis of a critical problem in applied ecology

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The Eurasian badger (*Meles meles*) is implicated in the transmission of bovine tuberculosis (TB) to cattle in the UK and Republic of Ireland. Badger culling has been employed for the control of TB in cattle in both countries, with varying results. Social perturbation of badger populations following culling has been proposed as an explanation for the failure of culling to consistently demonstrate significant reductions in cattle TB. Field studies indicate that culling badgers may result in increased immigration into culled areas, disruption of territoriality, increased ranging and mixing between social groups. Our analysis shows that some measures of sociality may remain significantly disrupted for up to 8 years after culling. This may have epidemiological consequences because previous research has shown that even in a relatively undisturbed badger population, movements between groups are associated with increases in the incidence of *Mycobacterium bovis* infection. This is consistent with the results from a large-scale field trial, which demonstrated decreased benefits of culling at the edges of culled areas, and an increase in herd breakdown rates in neighbouring cattle.

Keywords: behaviour; disease control; movement; social organization; wildlife disease reservoir

1. INTRODUCTION

Culling is frequently used as a tool for the control of diseases in wildlife populations (Wobeser 1994). The ultimate aim may be to eliminate the disease from the wildlife population by reducing host numbers below the threshold required for persistence of infection (Anderson 1991), although simply reducing the number of infected animals may be sufficient to reduce transmission to humans or livestock. Both goals rely on the hypothesis that transmission rates increase positively with population abundance. However, there is little empirical evidence for persistence thresholds in wildlife populations (Lloyd-Smith *et al.* 2005), and the relationship between transmission rates and host abundance may be nonlinear (Barlow 1996; Smith 2001). The concept of linear transmission may be too simplistic to adequately describe disease dynamics in many wildlife populations, owing to the confounding influence of ecological complexities such as social organization, compensatory reproduction and immigration (Lloyd-Smith *et al.* 2005). Field evidence for nonlinear relationships between host density and disease transmission have been found for bovine tuberculosis (TB) infection in the brushtail possum (*Trichosurus vulpecula*) in New Zealand (Caley *et al.* 1998), with nonlinear models providing more realistic simulations (Barlow 2000). Hence, attempts to manage disease by culling wildlife can have unpredictable consequences (Lloyd-Smith *et al.* 2005). The importance of culling-induced social perturbation to disease control was highlighted in the context of rabies control in the red fox (*Vulpes vulpes*; Macdonald & Bacon 1982). Simulation models have since predicted the effects of perturbation on the outcome of fox culling (Macdonald & Voigt 1985; Smith & Harris 1989), with subsequent support from empirical studies (Macdonald 1995).

The Eurasian badger (*Meles meles*) is considered to represent a significant wildlife reservoir for the transmission of *Mycobacterium bovis* (the causative agent of bovine TB) infection to cattle in the UK and Republic of Ireland (Muirhead *et al.* 1974; Bourne *et al.* 2007). In the UK, badgers were culled under a variety of strategies (see Krebs *et al.* 1997) between 1973 and 1998 with the aim of reducing infection in cattle. Despite some substantial reductions in the number of cattle herds testing positive for bovine TB (cattle herd breakdowns, CHBs) during the 1970s, since the mid-1980s the incidence of infection has continued to increase, particularly in southwest England (Department for Environment, Food & Rural Affairs (Defra) 2004, 2005). Field experiments suggest both positive and negative effects of badger culling on infection

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rates in cattle (Eves 1999; Donnelly *et al.* 2003, 2006; Griffin *et al.* 2005; Le Fevre *et al.* 2005). Social perturbation of badger populations following culling has been proposed as one explanation for the failure of some badger culling strategies to control TB in cattle (e.g. Overend 1980; Tuyttens & Macdonald 2000; Delahay *et al.* 2003; Donnelly *et al.* 2006, 2007).

2. WHAT IS SOCIAL PERTURBATION?

We define social perturbation as substantial disruption to the social organization and behaviour patterns of individuals in a population and propose three broad processes that may occur in badger populations in response to culling: (i) the vacuum effect: the tendency for individuals neighbouring a culled area to disperse inward to seek new home ranges (Macdonald 1995), which need not result in any increase in home range size or contact rates; (ii) territorial disruption: a breakdown of the discrete pattern of group territories typical of medium- to high-density badger populations (Kruuk 1978; Rogers *et al.* 1998). This may be accompanied by an increase in the frequency of movements of individuals between social groups; and (iii) the increased ranging behaviour of individuals in response to culling. Processes (ii) and (iii) may occur in both immigrant and residual populations following culling. Any of these processes may influence contact rates between badgers, potentially increasing disease transmission in the population, and/or the likelihood that infected animals become infectious through stress-induced immunosuppression (Gallagher & Clifton-Hadley 2000). Both phenomena could lead to an immediate increase in the risk of infection in cattle.

In this study, we conduct new analyses of long-term data from a badger population previously subjected to culling. We also review past studies of social perturbation and explore the wider literature to discuss the evidence for perturbation-induced disease transmission in badgers and cattle.

3. MATERIAL AND METHODS

(a) *Study design*

New analyses presented here were carried out on data from a previously well-described long-term study of a badger population in Woodchester Park, Gloucestershire (see Cheeseman *et al.* 1987), part of which (North Woodchester) was subjected to culling in 1978 and 1979 (Cheeseman *et al.* 1993). We calculated the group range size, extent of group range overlap and distance between main setts and bait marked returns between removed, neighbouring and all other social groups in North Woodchester to allow direct comparison with the results from four other published field studies on social perturbation in badgers (table 1). For comparative purposes we have used the definitions in Tuyttens *et al.* (2000*a*): 'removed' groups are those in which culling occurred; 'neighbouring' groups are those immediately adjacent to removed groups; and 'other' groups are those at least one social group away from removed groups. The social organization of badger populations can be investigated by bait marking, which involves feeding marked bait at setts and surveying for the indigestible coloured markers in latrines (Kruuk 1978; Delahay *et al.* 2000). Bait marking provides an estimate of the home range of a social group; it can identify annual changes in the size of group ranges and the degree of range exclusivity indicates the level of territoriality in the population. Social group ranges in the reviewed field studies were defined as the area included in either a 95% minimum convex polygon (MCP) around the outermost latrines (North Woodchester; Tuyttens *et al.* 2000*a*) or a 100% MCP (Roper & Lüps 1993; O'Corry-Crowe *et al.* 1996; Woodroffe *et al.* 2005), after excluding outlying bait returns in accordance with Delahay *et al.* (2000). This method may underestimate group range size where there are few bait returns, such as following culling. We therefore calculated the mean distance between a sett and its associated bait returns as an alternative measure in accordance with Tuyttens *et al.* (2000*a*) and Woodroffe *et al.* (2005). Group range size and overlap were determined using ArcGIS (Environmental Systems Research Institute (ESRI) 2005).

Previously unpublished data (S. P. Carter, 2006) on the number of colonizing adult and yearling badgers for 5 years following the removal in North Woodchester are presented in table 2 for comparison with other studies.

(b) *Data analysis*

The effect of badger removal operations on behaviour at the social group level at North Woodchester was investigated by fitting three statistical models in which the explanatory variable was the number of years since the group was culled (where appropriate), fitted as a categorical variable. Response variables were percentage range overlap (log transformed due to non-normality), mean group range size and mean distance between setts and bait returns. Data on all 39 social groups between 1977 and 1994 were included in the analysis. Data from setts or social groups located in close proximity to each other cannot be considered truly independent as they may be similar with respect to unmeasured ecological covariates. Potential spatial correlation was accounted for by dividing the study area into five similar sized zones and including zone as an explanatory factor in each model. Each zone contained between 6 and 11 spatially clustered social groups and two of the zones contained a mix of removed and neighbouring groups. To account for potential temporal correlation, a repeated measures analysis with first-order autoregressive structure was fitted to the responses from a given social group (Brown & Prescott 1999). In all models, calendar year was fitted as a categorical variable to account for any potential bias. All analyses were carried out using SPSS v. 15.0 (SPSS, Inc., Chicago, USA).

4. FIELD EVIDENCE OF SOCIAL PERTURBATION IN BADGER POPULATIONS

(a) *The vacuum effect: immigration and recolonization*

Following the complete removal of 11 social groups at North Woodchester, initial immigration into the culled area was rapid. However, it took 10 years for the population to recover to pre-removal density and the territorial configuration of neighbouring groups was unaffected (Cheeseman *et al.* 1993; figure 1). In a lower-density population at North Nibley, the near-complete (90%) removal of eight social groups also caused rapid immigration from neighbouring groups, but the latter were also severely disrupted, and the return to pre-cull density took only 5 years (Tuyttens *et al.* 2000*a*; Macdonald *et al.* 2006).

Table 1. Results of field studies investigating the impact of population reduction on the demography and social behaviour of badger populations. (n.s., non-significant; n.a., not applicable; n.d., no data available; d, density; s, social structure.)

study	no. of removal operations; year of removal(s)	method of removal	study area (removal area, km^2)	pre-removal density in study area (adults km^{-2})	no. of social groups in study area (no. targeted during removal)	no. of adult badgers removed from study area (% efficacy)	observed effects[a]	years to recovery
North Woodchester (Cheeseman *et al.* 1981, 1993; present paper)	1; 1978 and 1979 (two areas)	cage trapping and shooting; snaring	3 (3)	20	11 (11)	65 (100%)	initially rapid immigration by females increased group range overlap increased group range size increased inter-group movements increased distances moved	8–10 (d and s)
East Sussex (Roper & Lüps 1993)	1[b]; 1986	suspected poisoning	n.a.	n.d.	1 (1)	5 (71%)	initially rapid immigration by males increased group range overlap increased distances moved	2 (s)
East Offaly (O'Corry-Crowe *et al.* 1993, 1996)	3; 1989–1990	snaring	16 (738)	3	14 (14)	35 (69%)	slight increase in group range size (n.s.) increased distances moved	n.d.
North Nibley (Tuyttens *et al.* 2000*a*,*b*)	2; 1995–1996	cage trapping and shooting	16.5 (6.5)	4	21 (6 and 2)	29[c] (90%)	initially rapid immigration by young females increased group range overlap increased group range size decreased individual home range size	5 (d)
RBCT proactive and reactive culling areas (Woodroffe *et al.* 2005)	proactive 3–6, reactive 1–3; 1998–2004	cage trapping and shooting	proactive: 16×5 (*ca* 100×5), reactive: 16×4[d] ($<100\times4$)	n.d.	n.d.	1111 (adults and cubs); proactive: 948, reactive: 163 (n.d.)	increased group range overlap (proactive only, compared to experimental control) increased group range size (all culling areas, compared to experimental control)	n.d.

[a] Definitions of the effects observed are given in the text.
[b] Not the result of an official badger removal operation. The traumatic death of five out of seven badgers in a single group provided the opportunity to study social perturbation.
[c] 1995 cull only.
[d] Localized culling in the vicinity of farms experiencing cattle TB outbreaks within each 100 km^2.

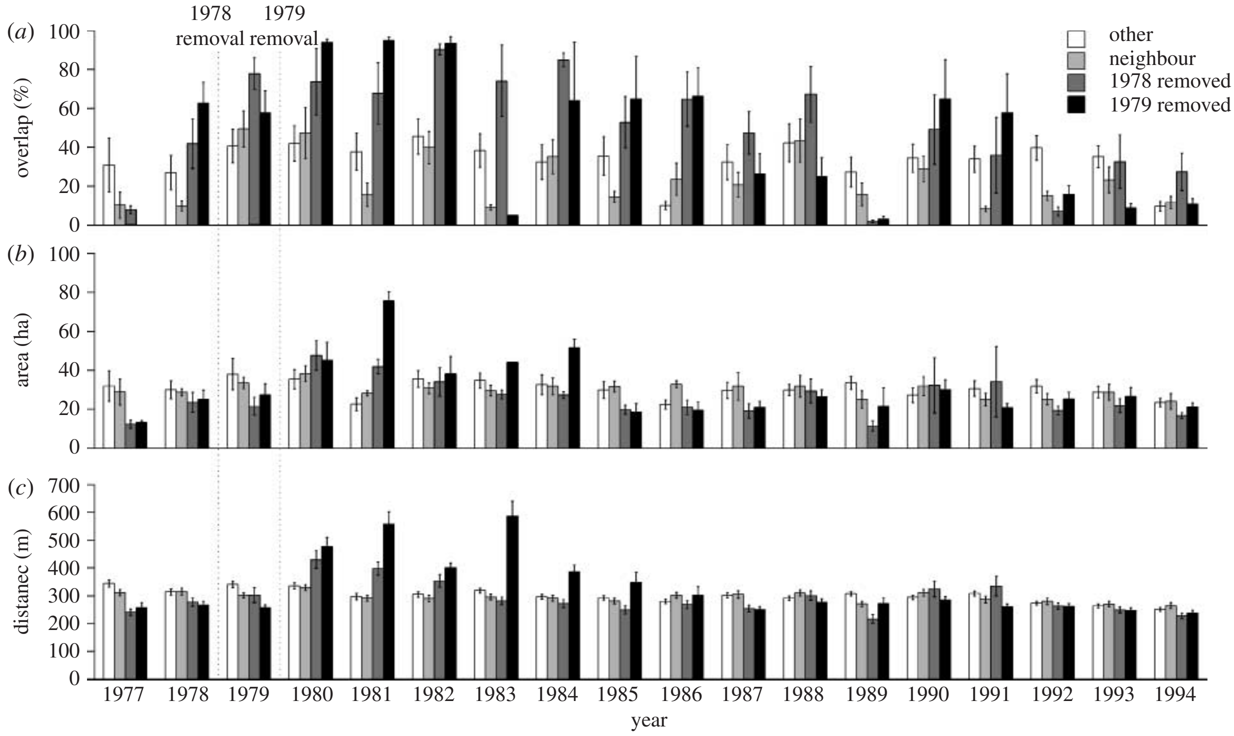

Figure 1. Mean and standard error of (*a*) percentage of social group range overlapping another group range, (*b*) area of social group range and (*c*) bait return distance for badger social groups in the North Woodchester removal area (1978 removed and 1979 removed) and for undisturbed groups throughout the Woodchester Park study area (neighbour and other).

Table 2. Age and sex structure of recolonizing badgers at North Woodchester following the complete removal of all badgers from 11 social groups in two successive culls in 1978 and 1979.

	male			female		
years after cull	adult	yearling	total	adult	yearling	total
1	1	1	2	5	1	6
2	0	0	0	0	0	0
3	1	0	1	1	0	1
4	0	0	0	0	0	0
5	2	2	4	0	1	1

Initial immigrants into culled areas at North Woodchester and North Nibley were almost exclusively adult and yearling females (table 2; Tuyttens *et al.* 2000*b*). In East Sussex, the removal by suspected poisoning of all the resident adult males in one social group was followed by frequent territorial incursions by males from neighbouring groups (Roper & Lüps 1993). The authors noted that neighbouring males were attempting to expand only into parts of the affected territory that were still occupied by the surviving females, whereas at North Woodchester and North Nibley immigrant females were first to occupy vacant habitat, which was only subsequently occupied by males (table 2; Tuyttens *et al.* 2000*b*). These findings concur with those from a long-term study of an undisturbed badger population at Woodchester Park where male badgers were more likely to move to groups with a greater proportion of adult females (Rogers *et al.* 1998). Rapid immigration was not reported in an intensive culling area in East Offaly, Republic of Ireland, possibly because it was largely surrounded by physical barriers to badger movement (O'Corry-Crowe *et al.* 1993). Movement patterns were not monitored outside this area, but the pattern of captures over the 6 years of the removal programme indicated that badgers were emigrating from the surrounding area (Eves 1999).

(b) *Territorial disruption*

All but one of the reviewed studies (table 1) showed either an increased group range overlap or a difference in overlap between culling treatments, strongly suggesting that culling disrupts territoriality. This was particularly evident following the complete removal of badger groups at North Woodchester (figure 1*a*; Cheeseman *et al.* 1993), where range overlap for removed groups was substantially larger than that of the neighbouring and other social groups ($F_{17,295}=3.5$, $p<0.001$; table 3). This persisted for at least 8 years after the cull, during which time the ranges of recolonizing badgers were not separated by distinct boundaries (Cheeseman *et al.* 1993). A similar pattern of group range overlap (an increase from 0.6 to 3.7% across all groups) followed culling at North Nibley (Tuyttens *et al.* 2000*a*). Although the magnitude of range overlap declined markedly within 2 years, overlap persisted for at least 4 years (Macdonald *et al.* 2006). Roper & Lüps (1993) reported that despite substantial range overlap with two adjacent groups occurring within four months of

Table 3. Results of the repeated measures analysis examining the effect of culling on subsequent group range size, percentage overlap between groups and mean distances between setts and bait marked returns for recolonizing badger groups at North Woodchester. Differences in the above parameters between removed groups (groups subjected to culling) each year up to 16 years post-culling were compared with those for the same groups 2 years prior to culling and for all other social groups for the whole 18-year period (referenced against a baseline of 0, i.e. no years post-cull). Significant *p*-values (at the 5% level) are shown in italic.

	group range			log group range overlap			bait return distance		
years after cull	β	t (d.f.)	p	β	t (d.f.)	p	β	t (d.f.)	p
1	9.86	2.03 (474)	*0.04*	1.86	4.29 (477)	*<0.0001*	83.82	3.11 (522)	*<0.01*
2	37.37	7.56 (410)	*<0.0001*	1.64	3.80 (447)	*<0.001*	159.47	5.87 (485)	*<0.0001*
3	14.29	3.05 (335)	*<0.01*	1.66	4.14 (404)	*<0.0001*	96.09	3.68 (454)	*<0.001*
4	9.36	1.74 (409)	0.08	1.53	3.21 (472)	*<0.01*	175.82	6.51 (471)	*<0.0001*
5	10.89	2.08 (364)	*0.04*	1.19	2.63 (437)	*<0.01*	27.16	1.0 (474)	0.32
6	−3.39	−0.64 (363)	0.52	1.26	2.75 (437)	*<0.01*	41.20	1.58 (447)	0.12
7	−7.27	−1.43 (341)	0.16	1.42	3.24 (421)	*<0.01*	−17.00	−0.63 (474)	0.53
8	−5.86	−1.20 (323)	0.23	0.94	2.24 (413)	*0.03*	−37.63	−1.44 (447)	0.15
9	−4.30	−0.89 (320)	0.38	0.76	1.89 (412)	0.06	−37.48	−1.44 (454)	0.15
10	1.45	0.29 (338)	0.77	0.37	0.87 (426)	0.39	−12.51	−0.48 (454)	0.63

the removal of all adult male badgers from one social group, mutually exclusive group ranges reappeared within 2 years. Differences in pre-removal density and the proportion of animals removed between the three studies may explain the observed variance in rates of return to the former social structure. Woodroffe *et al.* (2005) reported differences in group range overlap in a study comparing the spatial organization of badgers exposed to proactive (widespread and repeated culling throughout a treatment area) and reactive (local culling in response to a specific CHB) culling in 13 study areas within the randomized badger culling trial (RBCT; Bourne *et al.* 1998). The number of overlapping social group ranges varied significantly between culling treatments and was highest among groups up to 2 km outside the proactive treatment areas (median 1.4 versus 1.0 inside proactive areas). The median number of overlapping groups was lowest in reactive (0.6) and survey only areas (0.7). The number of overlapping group ranges increased following culling at North Nibley, but was unexpectedly highest among groups at least one social group from those removed (Macdonald *et al.* 2006).

Group range size appeared to increase following culling in four out of the five studies (table 1), although the effect was not statistically significant in one study (O'Corry-Crowe *et al.* 1996). There was a significant effect of culling on the size of removed group ranges at North Woodchester ($F_{17,297}=5.1$, $p<0.001$), with significant increases in the first three years and fifth year after culling (table 3 and figure 1*b*). Furthermore, there was a significant increase in the mean distance between the main sett and associated bait returns for removed groups ($F_{17,317}=6.5$, $p<0.001$), which persisted for 4 years after culling (table 3 and figure 1*c*). One year after the initial removal at North Nibley, bait marking revealed a 68% increase in the size of group ranges, while range size remained virtually constant in the undisturbed population at nearby Woodchester Park. The most pronounced increase was observed in those groups that were at least one group range away from the removed groups. Woodroffe *et al.* (2005) found that group ranges and distances between setts and bait returns were consistently larger in culled areas compared with experimental control areas. Moreover, outside culled areas, group range size increased with proximity to the culling area, revealing a gradation of social disruption.

In medium- to high-density badger populations, movement between social groups is restricted by the prevailing territorial system. Monitoring of the high-density Woodchester Park population suggests rates of permanent movement between social groups of 10% or less (Cheeseman *et al.* 1988; Rogers *et al.* 1998). Twenty-six per cent of all movements recorded by Cheeseman *et al.* (1988) occurred within the area disturbed following the complete removal of badgers in 1978 and 1979, even though it only supported approximately 12% of the total population (Cheeseman *et al.* 1993). At North Nibley, inter-group movements were more frequent as 18% of badgers moved to non-adjacent groups during the study, compared with only 4% at Woodchester Park during the same period (Tuyttens *et al.* 2000*b*). Furthermore, at North Nibley, a short-term increase in extra-group movements was observed in response to culling (Tuyttens *et al.* 2000*b*).

(c) *Increased ranging behaviour*

In three of the five reviewed studies (table 1; Cheeseman *et al.* 1993; Roper & Lüps 1993; Tuyttens *et al.* 2000*a*), the behaviour of individual badgers was investigated using radio-tracking, and in another (O'Corry-Crowe *et al.* 1996) it was derived from trapping data. In three studies, badgers were observed to have either moved greater distances or increased individual home range sizes following removal. One year after the removal of half the residents of 14 social groups from a 16 km^2 area in East Offaly (Eves 1999), badgers were observed to have moved significantly greater distances from their main setts (O'Corry-Crowe *et al.* 1996). Following the complete removal of badgers from North Woodchester, the home ranges of two colonizing adult females were five times larger than for females in an undisturbed part of the study area (Cheeseman *et al.* 1993). Following the removal of all the adult males from a group in East Sussex, the two remaining females spent approximately 30% of their active time outside their original group range, compared with only 5% before (Roper & Lüps 1993). Paradoxically, individual home range sizes decreased following the North Nibley badger removal, despite a substantial increase in group ranges revealed by bait marking (Tuyttens *et al.* 2000*a*). The reasons for this are unclear, although only a small subsample of the population was radio-collared, whereas a greater proportion may have had access to marked bait.

5. EPIDEMIOLOGICAL CONSEQUENCES OF CULLING BADGERS

(a) *Effects of culling on TB in badgers*

Field studies indicate some common responses to culling such as initial rapid immigration into culled areas and increased movements, although the precise characteristics and extent of these phenomena may vary. The epidemiological consequences of social perturbation are less clear. Only two of the five studies reviewed relate social perturbation to observed epidemiological effects. In North Woodchester, infection was not detected in badgers that colonized the culled area until 10 years later (Cheeseman *et al.* 1993), suggesting that the disease was brought into the area by recolonizing animals rather than arising from residual infection in the culled setts. Since the targeted groups were totally removed, there was no risk of infected badgers from within the culling area moving and exporting disease elsewhere. TB prevalence of badgers in the culled areas at North Nibley was considerably lower after culling and remained low for the following three years (Tuyttens *et al.* 2000*a*). The high culling efficacy of these two studies suggests that complete or virtually complete removal may have a beneficial impact on disease incidence in badgers (at least within the boundary of the culled area). The epidemiological consequences of highly efficient culls will depend on the likelihood that immigrant badgers will either bring infection with them or encounter and be susceptible to residual infection in the environment. Less efficient culling would be expected to lead to increased social perturbation of the residual badger population and decreased (even negative) disease control benefits. The clearest empirical support that culling may lead to increased prevalence of TB in badgers is provided by Woodroffe *et al.* (2006). An analysis of 7129 badgers killed in successive proactive culls during the RBCT showed that prevalence increased, particularly in areas where landscape features may have promoted recolonization by neighbouring badgers, and that prevalence increased more rapidly among badgers caught close to the boundary of the culled area. Further empirical support is provided by an 18-year study of 36 undisturbed social groups at Woodchester Park. The proportion of the population that moved between groups in 1 year was positively correlated with the incidence of new cases of *M. bovis* excretion in the following year (Rogers *et al.* 1998). Further work by Vicente *et al.* (2007) also showed that the risks of disease incidence among badgers were correlated with both individual and group-level movement. Although causation was not demonstrated in any of the above-mentioned studies, these associations are consistent with the hypothesis that increased movement increases contact rates between social groups and exacerbates disease transmission.

There are a number of factors that may have important consequences for perturbation but for which only limited data are available, and consequently cannot be explored in detail in this paper. For example, there will be a stochastic element to the removal of infected individuals during a culling operation such that an incomplete cull could result in removing none, few, most or all of the infected animals purely by chance. The density, demography and disease status of the population prior to culling may also influence subsequent perturbation effects and their epidemiological consequences. Furthermore, culling may directly alter the demographics of a population through compensatory reproduction (e.g. Heydon & Reynolds 2000). Consequently, while it might be possible to foretell the general territorial and behavioural consequences of culling, the demographic and epidemiological repercussions may be less predictable. In addition, the insensitivity of current methods to diagnose infection in live badgers (Pritchard *et al.* 1986; Clifton-Hadley *et al.* 1995*a*) and the potentially slow progression of disease in individuals (Gallagher *et al.* 1998) make detecting epidemiological patterns difficult.

(b) *Effects of culling on TB in cattle*

There is evidence from field studies in the UK and Republic of Ireland that badger culling influences the risks of infection in cattle (Clifton-Hadley *et al.* 1995*b*; Eves 1999; Griffin *et al.* 2005; Donnelly *et al.* 2003, 2006, 2007). The hypothesis that culling-induced social perturbation in badgers has epidemiological consequences provides a plausible explanation for some observed effects in cattle following badger culling. Two separate analyses (one of which included an additional year of data) of the incidence of CHBs in areas subjected to different badger culling treatments in the RBCT demonstrated that reactive culling was associated with a 25% increase in CHB incidence compared with no-culling areas (Donnelly *et al.* 2003; Le Fevre *et al.* 2005). The questionable benefit of badger culling for controlling TB in cattle was highlighted further by the observed consequences of proactive culling during the RBCT (Donnelly *et al.* 2006, 2007). Recently updated analyses show that there was an overall 23% reduction in CHB incidence inside proactive culling areas, but this was accompanied by a 25% increase in incidence in a surrounding 2 km wide buffer zone (Donnelly *et al.* 2007). Within the culled areas, there was a tendency for CHB incidence to increase with proximity to the boundary, although there was also a tendency for the negative effects of culling to diminish with successive annual culls. These results suggest that the negative impact of social perturbation of badger populations on the control of TB in cattle is strongest at the edges of the culled area. This would explain the results of the reactive treatment as it involved incomplete and scattered culling operations, which presumably produced a disproportionately large region within the treatment area that bordered culls.

In contrast, a number of large-scale, very intensive removal operations have demonstrated an association between the removal of badgers and a reduction in CHBs. The complete removal of badgers from a 104 km^2 area of exceptionally high cattle TB incidence in southwest England, and the continual removal of immigrants over a 6-year period, led to an apparent reduction in the incidence of CHBs compared with an adjacent area subjected to only small-scale badger removals (Clifton-Hadley *et al.* 1995*b*). A large-scale badger cull in East Offaly, Republic of Ireland, removed 1797 badgers from a 738 km^2 area over 6 years, with subsequently, significantly fewer CHBs in the removal area than in a surrounding area in which no systematic badger removals had taken place (Ó Máirtin *et al.* 1998; Eves 1999). Conversely, after the partial removal of badger groups (approx. 50%) from part of the East Offaly study area, there was a fivefold increase in herd prevalence (O'Corry-Crowe *et al.* 1996). A lack of replication and strict experimental controls in the East Offaly study casts doubt on the confidence with which the results could be attributed to the culling operations. A subsequent large-scale study compared the effects of two different badger culling strategies on the control of TB in four paired study areas in the Republic of Ireland (Griffin *et al.* 2005). Results indicated that the probability of a CHB was significantly lower in areas where badgers were proactively culled than in paired 'reference areas' where they were locally culled in response to a severe CHB. Although the magnitude of the effect of culling is compelling, it does not provide robust evidence that culling reduces CHBs as there was no experimental control with which to compare breakdown rates in the absence of culling.

6. IMPLICATIONS OF SOCIAL PERTURBATION FOR TB CONTROL IN CATTLE

Incomplete removal of badgers during localized culling operations appears to have at best no effect and at worst may cause an increase in CHBs (O'Corry-Crowe *et al.* 1996; Donnelly *et al.* 2003; Le Fevre *et al.* 2005). The observed increase in CHBs following reactive culling resulted in the premature cessation of this treatment in the RBCT and led to the conclusion that this approach offers no practical benefit to the control of TB in cattle (Bourne *et al.* 2005). In contrast, there is some evidence that the virtual elimination of badgers can lead to a reduction in CHBs within the culled area (Clifton-Hadley *et al.* 1995*b*; Eves 1999; Griffin *et al.* 2005; Donnelly *et al.* 2006, 2007). Nevertheless, where opportunities for badger immigration remain there will always be a risk of infection returning (see Cheeseman *et al.* 1993; Clifton-Hadley *et al.* 1995*b*). Furthermore, there is compelling evidence from field studies that social disruption of badger populations extends beyond the immediate vicinity of the targeted social groups (Tuyttens *et al.* 2000*a*; Woodroffe *et al.* 2005; Macdonald *et al.* 2006). Associated increases in the movement of infectious badgers and consequently increased contact with cattle provide the most parsimonious explanation for the relatively immediate increase in CHBs adjacent to proactive culling areas in the RBCT (Donnelly *et al.* 2006, 2007), leading to the conclusion by the Independent Scientific Group on Cattle TB that 'badger culling cannot meaningfully contribute to the future control of cattle TB in Britain' (Bourne *et al.* 2007).

Both the efficacy and scale of badger culling operations have varied widely with apparent consequences for social perturbation and it may be argued that increasing either might reduce the negative effects of perturbation. However, two separate analyses of trapping efficacy in the RBCT using quite different approaches demonstrated that the overall proportion of badgers removed from proactive culling areas was considerably higher than earlier estimations (Smith & Cheeseman 2007; Woodroffe *et al.* 2007). For example, after accounting for badgers removed from non-consent land by remote trapping, Smith & Cheeseman (2007) estimated that trapping efficacy in the initial culls ranged between 32 and 77% (versus 20–60%; Defra 2005), but importantly the negative effects of culling were consistent across this range (Donnelly *et al.* 2006, 2007). Furthermore, predictions from modelling suggest that increasing the culling efficacy from 80 to 100% would result only in a small reduction in CHBs (Smith *et al.* 2001), and in a recent theoretical analysis which ignored the effects of social perturbation (Smith *et al.* 2007) it was difficult to identify badger culling strategies that would lead to a substantial overall economic benefit, although large-scale culling was not evaluated. Thus, the inclusion of even modest levels of social perturbation would make economically beneficial badger culling strategies even harder to find. While the complete eradication of badgers from an area would eliminate the detrimental effect of increased movement by infected individuals who survived culling, immigration would still occur. More efficient culling could also increase potential opportunities for immigration, thereby creating a stronger vacuum effect.

Removing a large proportion of the resident badgers over a very large area may reduce some of the negative effects of perturbation, although there is no reliable scientific evidence to substantiate this. Updated analyses of the results from the proactive culling treatment in the RBCT indicate that culling areas need to be at least 80 km^2 and culled annually for 5 years in order for the benefits of culling to outweigh the increase in peripheral CHBs, assuming a circular culling area and a constant beneficial effect of culling throughout the culling area itself (Bourne *et al.* 2007). However, the 95% CIs surrounding this estimate suggest that it could require a culling area of at least 455 km^2 to achieve a net benefit of culling. Increasing the size of the proposed culling area would also most likely result in a concomitant increase in the total area of non-consent land. Despite the success of remote trapping in the RBCT (Donnelly *et al.* 2007), these regions represent additional potential sources of immigrants for culled areas.

7. CONCLUSIONS

Assumptions underlying the use of culling as a tool for the control of wildlife disease may be simplistic and take scant account of potentially important ecological processes. For example, the spatial structure and social organization of an intensively studied, high-density badger population have been demonstrated to have a profound influence on disease dynamics. The empirical evidence for social perturbation of badger populations following culling is extensive and suggests some consistent outcomes, including increases in the size and overlap of social group ranges, and increased movement and immigration. In addition, the extent of these effects may vary according to local conditions. The consequences of culling on infection in badger populations are however less clear, and at the scale of most field studies may be difficult to detect owing to stochastic variation. Nevertheless, the results of the RBCT show an effect of badger culling on subsequent CHB rates and therefore implicate the badger in the transmission of infection. However, these results suggest that the impact of badger culling on CHBs may be at best equivocal and at worst counterproductive. The epidemiological impact of social perturbation is the most plausible explanation for the observed counterproductive effects of badger culling. Of particular concern is the tendency for the perturbation effects discussed to extend to some distance from the culled area. It is essential that any proposed future strategy is thoroughly evaluated, taking consideration of the consequences of social perturbation, to ensure that it achieves the desired objective and does not impede the effective control of TB in cattle.

This paper includes some analysis of data derived from the live badger trapping programme at Woodchester Park. CSL operates an ethical review process for all work carried out on animals and all procedures are undertaken under Home Office licence and with the guidance and supervision of named vets and Named Animal Care and Welfare Officers (NACWOs).

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