A review of the evidence for culling-induced social perturbation and disease transmission in badger (*Meles meles*) populations.

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Summary

- Evidence suggests that TB infection in badgers is structured around social groups, with rates of infection between members of the same group being higher than between neighbouring groups. This probably reflects the stable and territorial nature of badger social structure in undisturbed moderate to high density populations.

- Perturbation events, such as culling, may disrupt the territorial organisation of badgers leading to increased ranging by individuals, enhanced movement and mixing between social groups. Field studies have demonstrated relatively consistent effects of increased ranging behaviour and dispersal following culling, but the precise nature of these effects differs from study to study and may be related to the age, sex and infection status of the removed and remaining badgers. Past culling and or illegal persecution and the frequency and duration of culling may also affect the extent of a perturbation effect

- Long-term studies of TB in an undisturbed badger population have shown a relationship between years of increased badger movement and subsequently higher disease incidence in the population.

- It is hypothesised that increased movement of badgers following a perturbation event such as culling could increase disease transmission rates between badgers and from badgers to cattle. However, there is currently no clear epidemiological evidence of such an effect. The full results of the RBCT and associated studies should provide further qualification and quantification of this effect.

- As a hypothesis, perturbation provides a possible explanation for a number of observed effects. These include the results of the reactive treatment within the RBCT which at best led to no decrease in TB breakdowns, at worst may have been associated with an increase.

- These phenomena need to be taken into consideration in the formulation of badger control strategies. In particular, small scale, piecemeal or intermittent culling strategies may be most at risk of significant perturbation effects, although such effects may still be important even at relatively high levels of culling efficiency. More information should become available at the end of the RBCT and upon completion of an associated ongoing perturbation study.

Background

Badgers in undisturbed medium to high-density populations in the UK live in relatively stable, social groups with clearly defined, discrete territories which mitigates against frequent movement between groups (Kruuk, 1978; Neal and Cheeseman, 1996). Consequently, the natural spread of disease between groups is low, compared to transmission within groups, and there is good observational evidence to support this (Cheeseman *et al*., 1988[a]; Delahay *et al*., 2000). Perturbation, such as badger culling operations, is believed to disrupt the territorial organisation of social groups resulting in increased movement of badgers. It is hypothesised that this increased badger movement and mixing can increase the opportunities for disease transmission (Overend, 1980; Rogers *et al*., 1998; Tuyttens *et al*., 2000[a]). Social disruption or perturbation of badger groups following culling has been proposed as one explanation for the failure of some badger culling strategies to control TB in cattle (Tuyttens and Macdonald, 2000; Donnelly *et al*., 2003). The existing evidence for culling-induced perturbation, its epidemiological consequences and the implications for lethal control of badgers are reviewed and discussed.

Field evidence of culling-induced social perturbation

There is strong evidence to suggest that badger removal operations can lead to increased movement and mixing between the survivors. Trapping operations undertaken to remove all badgers from two areas of TB outbreaks near Woodchester Park in Gloucestershire, during 1978 and 1979, provided an early opportunity to study this phenomenon (Cheeseman *et al*., 1993). Following the complete clearance of badgers from five social groups in Atcombe and six social groups in North Woodchester, all setts were reoccupied after three years, but there was considerable overlap of badger movements and no obvious territories were present. It took nine to ten years for the populations to recover to their pre-removal density and for their territorial organisation to stabilise to the pre-cull situation of discrete, non-overlapping territories. During the initial phase of recolonisation, social organisation was highly disrupted and badgers travelled over greater than usual distances. Slight increases in territory size were recorded and the mean distance from setts to boundary latrines increased sharply during the first two years following the culling operation with a gradual return to pre-cull distances after about five years. Radio-tracking observations of two colonising adult female badgers revealed that their home ranges were five times larger than typical ranges of females in an undisturbed part of the study area (Cheeseman and Mallinson, 1979; Cheeseman *et al*., 1993). The colonising individuals also used more setts than usual. A previous study on dispersal in badgers comparing data collected at Woodchester Park between 1976 and 1985 with that from a lower density badger population in Bristol from 1978 to 1985 showed significantly more frequent movements between groups in the latter population (28% compared with 5%, Cheeseman *et al*., 1988[b]). Interestingly, 26% of all recorded movements in Woodchester Park during this period occurred within the disturbed areas at Atcombe and North Woodchester, which supported a very small proportion of the total badger population.

An unusual opportunity to study perturbation arose when all of the male badgers died, believed to have been poisoned, from one of five neighbouring social groups forming part of a long-term study of badger behaviour and ecology in East Sussex (Roper and Lüps, 1993). Within three months of the deaths substantial overlap was evident between the territories of this and an adjacent group, which had previously been virtually non-overlapping. Six months later there was considerable overlap with the territory of a third group, but within two years of the initial disruption the territories of these three groups had reverted to their previously stable configuration i.e. contiguous with virtually no overlap. In addition radio-tracking revealed that the two surviving females from the depleted group ranged considerably further than they had before the perturbation event and spent around 30% of their active time outside the boundaries of their original territories versus 5% prior to the death of the males (Roper and Lüps, 1993).

Similar effects were observed by O’Corry-Crowe *et al*. (1996) in a study conducted alongside a large-scale badger removal operation in East Offaly, Ireland [The East Offaly Badger Research Project (EOP); Eves, 1993]. They studied the relationship and overlap between farms and badger territories in a 16 km^2 area within the 528 km^2 central Project Area of the

EOP. Approximately 50% of badgers were removed from 14 social groups in the smaller study area in 1989. Slight increases in territory size of borderline significance were observed between 1989 and 1990, along with significantly greater extra-territorial movements. There were also significant increases in the number of farms in contact with each social group, as well as the number of social groups in contact with each farm (O'Corry-Crowe *et al*., 1996). Badger movement patterns were not monitored outside the 16 km^2 intensive study area, but the pattern of capture over the six years of the main removal programme indicated that badgers were moving into the removal area from the surrounding experimental control area (Eves, 1999).

Further evidence of culling-induced perturbation was demonstrated following localised badger removal operations in North Nibley, Gloucestershire carried out in 1995 and 1996 (Tuyttens *et al*., 2000[a&b]). Twenty-seven badgers were removed from six out of a total of 21 social groups in the first year and a further two badgers were removed from two different social groups in the second year. Only three animals from two social groups are known to have survived the initial cull and the overall population level was reduced by approximately one third. The social organisation was consequently severely disrupted in the first year following culling, less so in the second year and in contrast to the findings of Cheeseman *et al*. (1993) the population had returned to its pre-removal density by the third year. This is also less than the recovery time of five years predicted by a simulation modelling exercise by Anderson and Trewhella (1985). Tuyttens *et al*. (2000[a]) postulated that the smaller scale of the North Nibley study combined with a slightly lower culling efficiency and lower pre-removal density were likely to have been responsible for the short recolonisation period. They also suggest that resident animals were more predisposed to move following the cull because this was a lower density population that had been disturbed by previous culls and therefore probably had a more fluid social structure than that at Woodchester Park. Mean group ranges (derived from bait-marking) increased by 68% in the year following culling and territories were difficult to define as there was considerable overlap, whereas territory sizes and configuration remained virtually constant in an undisturbed control site during the same period. The increase in mean group ranges did not appear to be from increased individual ranges, on the contrary individual home ranges (derived from radio-tracking) were smaller following culling. The authors postulated that the enlarged ranges were probably a result of higher extra-group excursions (indicated from trapping). Spatial disruption was evident among social groups from which badgers were removed, neighbouring social groups but also groups that were separated from "removed" groups by at least one social group. Counter-intuitively, disruption was most severe in the latter groups. The only explanation given was that because these groups were located in an area with the least woodland, they may have increased their ranges to accommodate more woodland when the opportunity arose.

Very recent evidence for culling-induced perturbation comes from a study by Riordan *et al*. (submitted[a&b]) conducted in a reactive treatment area of the randomised badger culling trial (RBCT). Seventy-seven badgers were removed from a 37.3 km^2 study area during four culling operations between 2002 and 2003. Culling efficiency was calculated to be between 35-44%. Following culling there was an observed increase in the overlap of group territories (as indicated by bait-marking), increased movement between social groups (revealed from trapping) and an increased overlap in individual home ranges (from radio-tracking). Social groups in the treatment area were classified as "removed" (targeted for removal), "neighbouring" (immediately adjacent to removed groups), and "other" (at least one social group away from removed groups). Social groups in a survey only area of the RBCT were also studied as an experimental control (undisturbed groups). The proportional overlap between removed and neighbouring groups increased, whilst that of other and undisturbed groups decreased. Animals from removed and other groups increased their nightly travel distances following culling, whereas no changes were observed for animals from neighbouring or undisturbed groups. Proportional overlap between individual ranges increased between neighbouring and other groups, but not for removed groups, and no changes in overlap were observed in undisturbed groups. Movements between social groups were rare (12 detected inter-group movements from 663 trapping events). Nine (75%) occurred in the treatment population following culling and only one inter-group movement was detected in the control population, although it is not clear what proportion of overall trapping was conducted in the control population. There were significant increases in fresh bite wounds in neighbouring and removed groups following culling and bite wounding was significantly more likely in males, especially cubs. However, the biggest increase in bite wounding was detected in the control population and no correlation was found between bite wounding and TB infection (Riordan *et al*., submitted[a]). A retrospective analysis of bite wounding data collected at North Nibley compared to two undisturbed badger populations, did not detect an overall change in the frequency of bites (Delahay *et al*., in press). However, there was some evidence that females were more likely to have bite wounds following culling.

Evidence for increased disease transmission following social perturbation

It is hypothesised that the increased movements of badgers following culling could lead to increased rates of disease transmission between badgers and between badgers and cattle. The evidence of this from field studies is, however, unclear.

The only study to clearly identify an association between increased badger movement and disease incidence is that by Rogers *et al*. (1998). The authors investigated the relationship between inter-group movements and disease incidence of 1,763 badgers from 36 social groups over an 18-year period as part of an intensive long-term study of a naturally infected high-density badger population in Woodchester Park. This revealed that incidence of *M. bovis* in badgers was significantly correlated with the pattern of movement over time, such that increased movement between groups in one year was followed by an increase in TB incidence in the following year. Although causation has not been shown, this is consistent with increased movement resulting in increased contact rates between members of different social groups and enhanced disease spread. It follows that TB incidence in cattle (assuming significant transmission from badgers) may take longer to become apparent.

Evidence for changes in disease transmission in badgers following removal operations is less clear. Following removal operations in Atcombe and North Woodchester *M. bovis* was not detected in either badger population until 10 years after the initial removal (Cheeseman *et al*., 1993). This time lag suggests that the disease was brought into the area by recolonising animals rather than resulting from residual infection in the setts of removed badgers. Because the targeted groups were totally removed there was no risk of infected badgers from within the culling area moving, and transporting disease, outside the area.

TB prevalence in badgers was considerably lower after the removal operation in North Nibley and remained low for the three years of the study (Tuyttens *et al*., 2000[a]). This is despite the considerable disruption observed following the culling operation. There may be a stochastic element to the removal of diseased individuals during a culling operation, such that even an incomplete cull might remove most or all of the diseased animals purely by chance. Equally, few or none of the diseased animals might be removed via the same process. Consequently, whilst it might be possible to predict general demographic and behavioural trends following a perturbation event, the epidemiological consequences may be less predictable. Hence, Riordan *et al*. (submitted[a]) found that TB prevalence in badgers increased in both the treatment and the control site following culling, but within the treatment area it declined in groups that were subjected to reactive culling and increased in neighbouring social groups. The authors argue that illegal culling in the control area could potentially account for this unexpected result but this remains speculation.

Simulation models constructed from empirical data have been used to examine the possible effects of badger culling on disease transmission (Smith *et al*., 2001[a&b]). However, by necessity these models include assumptions to cover areas of uncertainty e.g. transmission rates from badgers to cattle. Their continual improvement relies on the adjustment of parameters using data from empirical studies. White and Harris (1995) used a multiple parameter, spatially stochastic simulation model to describe the dynamics of TB in badgers in southwest England. Estimates of intra- and inter-group infection probabilities were obtained through repeated simulations based on field observations of the spread and prevalence of TB. The model identified a threshold group size of around six adult and yearling badgers beyond which the probability of disease spread and persistence increased. They postulate that increased inter-group movement arising from perturbation is likely to reduce the threshold group size to well below this threshold value. Whilst acknowledging the lack of quantitative data on the extent to which social perturbation does act to promote transmission, Swinton *et al*. (1997) used a simple deterministic model to demonstrate that perturbation effects may reduce the effectiveness of lethal control, making other control measures (e.g. fertility control) more effective.

In summary, evidence for a direct and causative link between social perturbation and increased disease transmission is equivocal. There is strong evidence for a link between rates of social movement and disease incidence in an undisturbed population, but epidemiological evidence following badger culling is less clear. More information on this topic will be forthcoming once the results of the RBCT are available.

Evidence for the effects of badger culling on rates of cattle herd breakdown

The hypothesis that culling-induced social perturbation may increase rates of disease transmission provides a possible explanation for a number of observed effects following culling operations.

Donnelly *et al*. (2003) compared TB incidence rates in cattle herds subjected to different treatments in the RBCT (localised reactive culling, proactive culling, no culling). This showed that reactive culling was associated with a 27% increase in incidence of CHBs versus no culling. This finding led to the cessation of the reactive element of the RBCT and for the Independent Scientific Group on Cattle TB to conclude that reactive culling, in the form implemented in the RBCT, offers no practical benefit to the control of TB (Bourne *et al*., 2004). Donnelly *et al*. (2003) hypothesise further that national badger culling strategies prior to the start of the RBCT may have been similarly ineffective, referring to the rise in TB incidence in cattle from 0.75% in 1986 to 2.61% in 1996. Perturbation effects were suggested as a possible cause for the observed increase in TB incidence in the reactive areas of the RBCT. However, it is questionable whether there would have been sufficient time between the culling and the herd breakdowns for perturbation alone to explain the observed increase in incidence.

In an independent scientific review of the RBCT Godfray *et al*. (2004) point out that the wide confidence interval (2% decrease to a 65% increase) around the quoted increase of 27% by Donnelly *et al*. (2003) indicates that the observed increase may have occurred purely by chance and conclude that this result should not be viewed as evidence for or against perturbation induced TB transmission. Godfray *et al*., (2004) also speculate on the importance of illegal culling in no culling areas of the RBCT, which if substantiated could partly explain the observed differences between TB incidence in the reactive and no culling areas.

The large-scale removal programme in East Offaly removed 1,797 badgers from a 738 km^2 area between 1989 and 1995 (Ó Máirtin *et al*., 1998) although it is unclear what proportion of the original badger population were removed during this programme . There were subsequently significantly fewer cattle herd breakdowns (CHBs) in the removal area than in a surrounding control area in which no legal culling had taken place (Ó Máirtin *et al*., 1998; Eves, 1999). This lends support to the effectiveness of badger culling in reducing TB outbreaks in cattle, however, the authors make it clear that conclusions should be drawn from this with caution as it was designed as an observational study without statistical replication. After the partial removal of badger groups (*c*.50%) from a restricted area in East Offaly (where population size was estimated prior to the removal) there was a fivefold increase in herd prevalence (O'Corry-Crowe *et al*., 1996). However, this increase cannot be attributed to the culling operation owing to the lack of an experimental control.

The East Offaly Project was followed by the "Irish Four Areas Trial" which attempted to assess the impact of two different badger removal strategies on the control of TB in a wider range of farming environments in Ireland (Griffin *et al*., 2004). The study found that the probability of a CHB was significantly lower in "Removal Areas", where badgers were proactively culled than in "Reference Areas" where badgers were reactively culled, and attributed this difference to the different culling strategies. However, this study does not provide evidence that either strategy reduces cattle herd breakdowns as there was no experimental control with which to compare breakdown rates. A subsequent analysis of the clustering of different strains of *M.Bovis* in badgers and cattle in the above study area suggested that social perturbation may have been responsible for the observed absence of shared clusters between badgers and cattle (Olea-Popelka *et al*., 2005).

Local variability of perturbation effects

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It seems reasonable to postulate that the higher the level of badger removal achieved, the more infected cases will be removed and hence the greater the benefit in terms of disease control. This is consistent with the idea that population density relates in a linear fashion to disease prevalence and incidence. However, at the range of badger densities observed at Woodchester Park, no such relationship was found (Cheeseman *et al*., 1988[a]; Rogers *et al*., 1999). In addition, field studies of perturbation suggest that the effects of culling are non-linear and often unpredictable (Tuyttens *et al*., 2000[a&b]; Riordan *et al*., submitted[a&b]). This may be related to the age, sex and infection status of the removed and remaining animals (Tuyttens *et al*., 2000[a&b]; Riordan *et al*., submitted[a]). After the removal at North Nibley adult females were more likely to lactate than those in an undisturbed population at Woodchester Park (Tuyttens *et al*., 2000[b]). The number of cubs per lactating female and reproductive rates were also higher at North Nibley than Woodchester Park two years after the cull (Tuyttens *et al*., 2000[b]). Riordan *et al*. (submitted[a]) similarly reported an increased number of reproductively active females in removed groups after culling. This suggests that culling removes reproductive suppression among female badgers.

Tuyttens *et al*., 2000[b] suggested that demographic changes due to culling might affect the susceptibility of the population to infection. Disease prevalence tends to be greater and progresses more rapidly in males (Cheeseman *et al*., 1989; Wilkinson *et al*., 2000), and cubs may potentially be more susceptible to infection because of pseudo-vertical transmission, risk-prone behaviour and an underdeveloped immune system. Therefore, changes to the sex and/or age structure of the population following culling may result in significantly different levels of TB prevalence.

It is also likely that the extent of the perturbation effect will be related to the degree of culling or other illegal persecution that had taken place in the past, as indicated by the substantially different recolonisation periods observed between the population at North Nibley and Woodchester Park. Populations that are already disturbed may potentially show very little change following further disturbance. The effects of perturbation may also be masked by other changes affecting rates of infection in badgers or cattle, for instance following the movement of infected cattle. The frequency and duration of badger control, either short periods of control followed by population recovery, or more continual control, may also influence the extent of perturbation.

How might perturbation effects vary with the geographic scale of culling??

Tuyttens *et al*. (2000[a]) found that perturbation effects were evident in groups that were one or more social groups away from removed groups suggesting that the consequence of culling may reach beyond the immediate social group involved.. If the main effect of culling-induced perturbation were from increased immigration of diseased animals into the culled area, perturbation effects would be expected to decrease with an increase in the scale of the operation. However, there are no available data to quantify or even confirm this and much of the evidence of culling-induced perturbation relates to increased movement by surviving individuals of social groups subjected to culling. Therefore, the efficacy of the culling operation appears to be equally, or even more, important than the scale of the operation. Evidence from the Irish four areas study and similar removal studies suggests that the virtual elimination of badgers by wide scale and intensive culling can lead to a reduction in CHBs (Clifton-Hadley *et al*., 1995; Eves, 1999; Griffin *et al*., 2005). However, unless the badger population is actively maintained at permanently low levels there is the risk of infection returning via immigration as reported by Cheeseman *et al*. (1993). The incomplete removal of badgers through localised culling operations, as conducted within the reactive treatment of the RBCT, 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; Riordan *et al*., submitted[a]).

There are currently insufficient data to quantify either the scale or the efficiency at which culling needs to be carried out in order to render any perturbation effect non-significant. We know that if badgers were eradicated from an area then this would, by definition, reduce inter-group movements; although recolonisation and edge effects would remain, these in turn would be reduced if culling were carried out at a large scale. However, although it seems intuitive that removing a very large proportion of the resident badgers over a large area will reduce perturbation effects, there is no reliable scientific evidence on which to base this assumption. These phenomena need to be taken into consideration in the formulation of badger control strategies. In particular, small scale, piecemeal or intermittent culling strategies may be most at risk of significant perturbation effects, although such effects may still be important even at relatively high levels of culling efficiency. More information should become available at the end of the RBCT and upon completion of an associated ongoing perturbation study.

References

Anderson, RM and Trewhella, W. 1985. Population dynamics of the badger (*Meles meles*) and the epidemiology of bovine tuberculosis. *Philosophical Translations of the Royal Society, London Series B* 310: 327-381.

Cheeseman CL and Mallinson PJ. 1979. Radio-tracking in the study of bovine tuberculosis in badgers. In: Amlaner CJ and Macdonald DW (eds.) *A handbook on radiotelemetry and radio tracking.* Pergamon Press, Oxford, p. 649-656.

Cheeseman CL, Wilesmith JW, Stuart FA and Mallinson PJ. 1988[a]. Dynamics of tuberculosis in a naturally infected badger population. *Mammal Review* 18(1):61-72.

Cheeseman CL, Cresswell WJ, Harris S and Mallinson PJ. 1988[b]. Comparison of dispersal and other movements in two badger (*Meles meles*) populations. *Mammal Review* 18:51-59.

Cheeseman CL, Wilesmith JW and Stuart FA. 1989. Tuberculosis: the disease and its epidemiology in the badger, a review. *Epidemiology and Infection* 103:113-125.

Cheeseman CL, Mallinson PJ and Wilesmith JW. 1993. Recolonisation by badgers in Gloucestershire. In: Hayden TJ (ed.) *The badger*. Royal Irish Academy, Dublin. p. 78-93.

Clifton-Hadley RS, Wilesmith JW, Richards MS, Upton P and Johnston S. 1995. The occurrence of *Myobacterium bovis* infection in cattle in and around an area subject to extensive badger control. *Epidemiological Infection* 114:179-193.

Delahay RJ, Brown J, Mallinson PJ, Spyvee PD, Handoll D, Rogers LM and Cheesman CL. 2000. The use of marked bait in studies of the territorial organization of the European badger (*Meles meles*). *Mammal Review* 30:73-88.

Delahay, RJ, Walker, N, Forrester, GJ, Harmsen B, Riordan P, Macdonald DW, Newman C and Cheeseman CL. in press. Demographic correlates of bite wounding in European badgers (*Meles meles* L.) in stable and perturbed populations. *Animal Behaviour*.

Donnelly CA, Woodroffe R, Cox DR, Bourne J, Gettinby G, Le Fevre AM, Mclnerney and Morrison WI. 2003. Impact of localized badger culling on tuberculosis incidence in British cattle. *Nature* 426:834-837.

Eves JA. 1993. Impact of badger removal on bovine tuberculosis in east County Offlay. *Irish Veterinary Journal* 52(4):199-203.

Griffin JM, Williams DH, Kelly GE, Clegg TA, O'Boyle IO, Collins JD and More SJ. 2005. The impact of badger removal on the control of tuberculosis in cattle herds in Ireland. *Preventative Veterinary Medicine* 67:237-266.

Godfray CJ, Curnow RN, Dye C, Pfeiffer D, Sutherland WJ and Woolhouse MEJ. 2004. Independent scientific review of the randomised badger culling trial and associated epidemiological research. *Report to Mr. Ben Bradshaw M.P. Central Science Laboratory,* York, 4 March 2004.

Kruuk H. 1978. Spatial organisation and territorial behaviour of the European badger (*Meles meles*). *Journal of Zoology* 184:1-19.

Neal E and Cheeseman CL. 1996. *Badgers*. T and AD Poyser Ltd., London. p. xiv-271.

O'Corry-Crowe, GO, Hammond R, Eves J and Hayden TJ. 1996. The effect of reduction in badger density on the spatial organisation and activity of badgers *Meles meles l.* in relation to farms in central Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy 96B*(3):147-158.

Ó Máirtin DO, Williams DH, Griffen JMm Dolan LA and Eves JA. 1998. The effect of a badger removal programme on the incidence of tuberculosis in an Irish cattle population. *Preventative Veterinary Medicine* 34:47-56.

Olea-Popelka FJ, Flynn O, Costello E, McGrath G, Collins JD, O'Keeffe J, Kelton DF, Berke O and Martin SW. 2005. Spatial relationship between *Mycobacterium bovis* strains in cattle and badgers in four areas in Ireland. *Preventative Veterinary Medicine* 71: 57-70.

Overend ED. 1980. Badgers and TB – Does gassing spread the disease? *Oryx* 15:338-240.

Riordan P, Macdonald DW, Delahay RJ, Cheeseman CL, Service K, Fordham E and Harmsen BJ. submitted[a] The impact of culling on Eurasian badger (*Meles meles*) populations and the epidemiology of bovine tuberculosis: 1. demography and social organisation.

Riordan P, Macdonald DW, Delahay RJ, Cheeseman CL, Service K, Fordham E and Harmsen BJ. submitted[b] The impact of culling on Eurasian badger (*Meles meles*) populations and the epidemiology of bovine tuberculosis: 2. Individual movement and dispersal.

Rogers LM, Delahay R, Cheeseman CL, Langton S, Smith GC and Clifton-Hadley RS. 1998. Movement of badgers (*Meles meles*) in a high-density population: individual, population and disease effects. *Proceedings of the Royal Society London Series B* 265:1269-1276.

Rogers LM, Delahay RJ, Cheeseman CL, Smith GC and Clifton-Hadley RS. 1999. The increase in badger *(Meles meles*) density at Woodchester Park, south-west England: a review of the implications for disease (*Myobacterium bovis*) prevalence. *Mammalia* 63(2):1830192.

Roper TJ and Lüps P. 1993. wissenschaftliche Kurzmitteilung. Disruption of territorial behaviour in badgers *Meles meles. Zeitschrift für Säugetierkunde* 58:252-255.

Smith GC, Cheeseman CL, Clifton-Hadley RS and Wilkinson D. 2001[a]. A model of bovine tuberculosis in the badger *Meles meles*: an evaluation of control strategies. *Journal of Applied Ecology* 38(3):509-519.

Smith GC, Cheeseman CL, Wilkinson D and Clifton-Hadley RS. 2001[b]. A model of bovine tuberculosis in the badger *Meles meles*: the inclusion of cattle and the use of a live test. *Journal of Applied Ecology* 38(3):520-535.

Swinton J, Tuyttens F, Macdonald D, Nokes DJ, Cheeseman CL and Clifton-Hadley, R. 1997. A comparison of fertility control and lethal control of bovine tuberculosis in badgers: the impact of perturbation induced transmission. *Philosophical Translations of the Royal Society, London Series B* 352: 619-631.

Tuyttens FAM and Macdonald DW. 2000. Consequences of social perturbation for wildlife management and conservation. In: Gosling M and Sutherland W (eds.) *Behaviour and Conservation*. Cambridge University Press, Cambridge. p. 315-329.

Tuyttens FAM, Delahay RJ, Macdonald DW, Cheeseman CL, Long B and Donnelly CA. 2000[a]. Spatial perturbation caused by a badger (*Meles meles*) culling operation: implications for the function of territoriality and the control of bovine tuberculosis (*Myobacterium bovis*). *Journal of Animal Ecology* 69: 815-828.

Tuyttens FAM, Delahay RJ, Macdonald DW, Cheeseman CL, Long B and Donnelly CA. 2000[b]. Comparative study on the consequences of culling badgers (*Meles meles*) on biometrics, population dynamics and movement. *Journal of Animal Ecology* 69: 567-580.

White, PCL and Harris, S. 1995. Bovine tuberculosis in badger (*Meles meles*) populations in southwest England: the use of a spatial stochastic simulation model to understand the dynamics of the disease. *Philosophical Translations of the Royal Society, London Series B* 346: 391-413.

Wilkinson D, Smith GC, Delahay RJ, Rogers LM, Cheeseman CL, Clifton-Hadley RS. 2000. The effects of bovine tuberculosis (*Mycobacterium bovis*) on mortality in a badger (*Meles meles*) population in England. *Journal of Zoology* 250:389-395.