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Effect of culling and vaccination on bovine tuberculosis infection in a European badger (*Meles meles*) population by spatial simulation modelling

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ABSTRACT

The control of bovine tuberculosis (bTB) in cattle herds in the Republic of Ireland (ROI) is partially hindered by spill-back infection from wild badgers (*Meles meles*). The aim of this study was to determine the relative effects of interventions (combinations of culling and/or vaccination) on bTB dynamics in an Irish badger population. A spatial agent-based stochastic simulation model was developed to evaluate the effect of various control strategies for bovine tuberculosis in badgers: single control strategies (culling, selective culling, vaccination, and vaccine baits), and combined strategies (Test vaccinate/cull (TVC)), split area approaches using culling and vaccination, or selective culling and vaccination, and mixed scenarios where culling was conducted for five years and followed by vaccination or by a TVC strategy. The effect of each control strategy was evaluated over a 20-year period. Badger control was simulated in 25%, 50%, and 75% area (limited area strategy) or in the entire area (100%, wide area strategy). For endemic bTB, a culling strategy was successful in eradicating bTB from the population only if applied as an area-wide strategy. However, this was achieved only by risking the extinction of the badger population. Selective culling strategies (selective culling or TVC) mitigated this negative impact on the badger population's viability. Furthermore, both strategies (selective culling and TVC) allowed the badger population to recover gradually, in compensation for the population reduction following the initial use of removal strategies. The model predicted that vaccination can be effective in reducing bTB prevalence in badgers, when used in combination with culling strategies (i.e. TVC or other strategies). If fecundity was reduced below its natural levels (e.g. by using wildlife contraceptives), the effectiveness of vaccination strategies improved. Split-area simulations highlighted that interventions can have indirect effects (e.g. on population size) in non-treatment areas. Our model suggests that mixed control strategies could maintain infection prevalence to a low level for a considerable period even with a growing population. The model supported the hypothesis that culling strategies appeared to be the most effective method for the control of bTB in badgers using parameters, where available, from ROI, either singly or in combination with other strategies. In this model, the success of a vaccination strategy depended partially upon population density and the proportion of the population infected, therefore an initial culling program (to reduce density and/or remove infected badgers) followed by long-term vaccination may be effective in controlling bTB in badgers.

1. Introduction

Bovine tuberculosis (bTB) is an infectious disease caused by *Mycobacterium bovis*. It is considered as one of the greatest challenges cattle farming faces in Britain and Ireland due to production loss, livestock deaths, and trade restrictions (Sheridan, 2011). It is also a zoonotic disease and a public health risk (O'Reilly and Daborn, 1995; Gallagher and Clifton-Hadley, 2000; Thoen et al., 2006).

In the Republic of Ireland (ROI), badgers, like cattle, are considered a “maintenance host” for *M. bovis* (More and Good, 2006; Corner et al., 2008a). In 1988, the Eradication of Animal Diseases Board of the ROI (ERAD) commissioned a report, ‘Badgers and

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Bovine Tuberculosis in Ireland' (O'Connor and O'Malley, 1989) in which it was concluded that badgers acted as a reservoir of infection and were likely an underlying driving factor causing difficulties in achieving eradication of bTB (More, 2005). Afterwards, two field studies were established to assess the relationship between tuberculosis in cattle herds and badgers; the East Offaly project (1989–1995; Eves, 1999), followed up by the Four Area project (1997–2002; Griffin et al., 2005). In both studies, intensive proactive culling lowered the risk of cattle herd breakdowns in removal areas, compared with reference areas which underwent very limited reactive culling (Eves, 1999; Griffin et al., 2005; Kelly et al., 2008). Furthermore, these culling efforts significantly lowered the herd breakdown risk for up to a decade after the end of the trial relative to reference areas (Byrne et al., 2014a). Studies of *M. bovis* strain types demonstrated that badgers and cattle can carry identical strains of *M. bovis* (Costello et al., 1999; Biek et al., 2012), indicating the occurrence of frequent cross-species transmission (Biek et al., 2012). Despite the intensive control efforts which are aimed at early detection and prevention of cattle-to-cattle transmission, bTB remains an ongoing problem in ROI (More and Good, 2006). Such cattle control efforts have led to bTB eradication in countries like Sweden, Norway, Denmark and The Netherlands, which are officially bovine tuberculosis free and are absent of a significant wildlife reservoir (Gortázar et al., 2012).

Due to the role of badgers in cattle bTB-epidemiology, badger populations in ROI have been subjected to a culling regime (non-selective cull of badgers initiated in 2004) directed to areas with a chronic history of tuberculosis in cattle herds (termed the "medium term" strategy; O'Keeffe, 2006). Culling intends to reduce the density of infected badgers, in anticipation of minimizing the transmission from badger-to-badger and spill over from badger-to-cattle. The lesion rate of cattle bTB in ROI, as confirmed at slaughter, has fallen from 20.7 in 2004 to 13.3 per 10,000 in 2011, a reduction of 30% (Council of Europe T-PVS/PA, 2012). This decline has been partially attributed to this "medium term" culling program, in combination with other cattle herd preventive measures (Sheridan et al., 2014).

Although badger culling is considered an effective strategy in reducing the density of diseased badgers in the ROI, it is also associated with animal welfare concerns and strongly opposed by a minority of public opinion (Eves, 1999; Griffin et al., 2005; O'Keeffe, 2006; Kelly et al., 2008). From this perspective, vaccination with Bacille Calmette-Guérin (BCG) is considered to be a practical and socially acceptable alternative method for controlling tuberculosis in badgers. BCG vaccine induces a protective effect in captive badgers after subcutaneous, mucosal and oral vaccination (Corner et al., 2008b; Lesellier et al., 2009; Corner et al., 2010). However, little information is available about the impact of wild badger vaccination on the control of bTB. Field trials in Ireland will help in answering questions related to the feasibility and effects of oral and intramuscular administration methods of BCG vaccine (Aznar et al., 2011; Byrne et al., 2012a, 2013a; Buddle and de Lisle, 2014).

Simulation models have been used to assess the effectiveness of bTB control strategies in badger populations (White and Harris 1995a,b; White et al., 1997; Smith et al., 1997, 2001, 2012, 2013). Data used in most of these models were generally derived from high density badger populations in UK (e.g. Woodchester park study population with a reported density of >25 km^{-2}; Rogers et al., 1997) which may not always be applicable to lower density badger populations in Ireland. In a number of these models, culling based strategies showed superior effectiveness in bTB control compared with vaccination (White and Harris 1995b; Barlow, 1996; Smith and Cheeseman, 2002). Using a density dependent model, it has been demonstrated that the birth of new susceptible badgers during vaccination campaigns makes it hard to maintain the population below the critical threshold density to maintain infection (Smith and Cheeseman, 2002). However, if culling leads to social perturbation which in turn could lead to increases in contact rates (amongst badgers) and increased transmission, it may generate only small reductions, or even increases in bTB prevalence ("the perturbation hypothesis"; Donnelly et al., 2006; Carter et al., 2007; Smith et al., 2012). In ROI, there is limited evidence in support of a perturbation effect increasing risk to cattle, as has been described in Great Britain (Corner et al., 2008a; Olea-Popelka et al., 2009; Sheridan, 2011). While culling may affect badger social structure (O'Corry-Crowe et al., 1996), there is no evidence yet presented that this consistently leads to increased prevalence within culled badger populations (Corner et al., 2008a; Byrne et al., 2015a) and subsequently to transmission to cattle (Olea-Popelka et al., 2009).

The aim of this research is to assess the relative effects of culling and/or vaccination on bTB dynamics in the badger population under Irish conditions. For this, a model that encapsulates population and disease transmission dynamics of an isolated badger population was developed.

2. Methods

2.1. Model framework

A stochastic, spatially explicit, agent-based model was developed using Netlogo software (Wilensky, 1999). The model operated on a hexagonal grid cell basis. The main grid contained 100 hexagonal cells, with each cell representing one badger territory occupied by a single group of badgers (social group). Each cell contained one main sett (a sett is a badger burrow complex; a main sett is a large sett, usually one per social group; Byrne et al., 2012b), in which breeding occurred. Due to the hexagonal nature of the grid, each territory had six neighbors (six social groups) directly sharing its borders. Details of the default parameters used is presented in the Supplementary material Appendix A, Table A.1.1.

2.2. Model structure and output

The N badgers in the model population were assumed to be in either susceptible (S), latent or exposed (L) or infectious (I) state. Individual badgers were characterized by the variables: sex (male or female), age (cubs if less than one year old and adults if over one year old), and bTB-state (S, L or I).

The model disregarded any possible external sources of infection such as infection from cattle, i.e. the badger population was assumed to represent an isolated population. Stuart (2010) studied reproductively successful females in ROI and concluded that the highest success rate was in groups with one or two breeding females. Thus, the model assumed a maximum of two adult females to be able to breed in each group in any given year. Cubs are born during January–March with most parturitions occurring in late January and February (Yamaguchi et al., 2006; Stuart, 2010). Thus, births were simulated during the first month of the model-year as a 'pulse' every year. Litter size was given by a Poisson distribution for a mean of 2.47 and the sex ratio of the population was kept at 1:1 (Anderson and Trewhella, 1985; Stuart, 2010). Natural mortality rates were taken from Smith et al. (2013). Cubs up to two months pre-emergence (i.e. prior to emerging from the sett) had a higher mortality rate compared to older badgers (Smith et al., 2013; Graham et al., 2013) (Supplementary Table 1). Badger dispersal behaviour in Ireland was assumed to be sex dependent; males having higher movement frequency compared to females (Byrne et al., 2014b). Dispersal rates were taken from the model of White and Harris (1995a) (Supplementary Table A.1.1.), and represented the non-temporary movement of adult badgers from their home social-group to another recipient social-group territory. Only adult