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Review

An ecological and comparative perspective on the control of bovine tuberculosis in Great Britain and the Republic of Ireland

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A B S T R A C T

Disease ecology involves a systematic approach to understanding the interactions and evolution of host–pathogen systems at the population level, and is essential for developing a comprehensive understanding of the reasons for disease persistence and the most likely means of control. This systems or ecological approach is being increasingly recognised as a progressive method in disease control and is exploited in diverse fields ranging from obesity management in humans to the prevention of infectious disease in animal populations. In this review we discuss bovine tuberculosis (bTB) in Great Britain (GB) within a disease ecology context, and suggest how a comparative ecological perspective helps to reconcile apparent conflicts with the evidence on the effectiveness of badger culling to assist in the control of bTB in GB and the Republic of Ireland (ROI).

Our examination shows that failure of past measures to control bTB and the disparity in outcomes of badger culling experiments are the result of a complex relationship amongst the agent, host and environment, i.e. the episystem, of bTB. Here, we stress the role of distinctive bTB episystems and badger culling trial design in the ambiguity and resulting controversy associated with badger culling in GB and ROI. We argue this episystem perspective on bTB control measures in cattle and badger populations provides a useful and informative perspective on the design and implementation of future bTB management in GB, particularly at a time when both scientific and lay communities are concerned about the ongoing epidemic, the cost of current control measures and the execution of future control procedures.

1. An episystem perspective on infectious disease control

Conventional principles of disease control involve the manipulation of the epidemiological triad of determinants of disease, classified as agent, host and environment, to halt the spread of infection (Thrusfield, 2005). However, this is often an inadequate representation of the underlying complexity of infectious disease dynamics. Few diseases exclusively affect only one species or a group of hosts (Daszak et al., 2000; Cleaveland et al., 2001), and these host populations are themselves embedded within dynamic ecological systems and subject to complex behavioural interactions. The often sensitive interactions that govern the regulation of disease mean that any change to the disease ecosystem can perturb the balance of host, agent and environment. Disturbances to these systems can result in outbreaks of disease (e.g. zoonotic cases of hantavirus pulmonary syndrome and nephropathia epidemica, Engelthaler et al., 1999; Tersago et al., 2009), yet historically

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such changes have also assisted in the control of certain diseases (e.g. malaria in England, Dobson, 1980).

Reductionist methods of disease control involve the removal of infection or the infectious agent by treating or culling, implementing barriers to direct and indirect transmission or by increasing inherent or acquired immunity to the infectious agent. However, for those diseases which evade such methods of conventional control, a more comprehensive understanding of the complex interactions amongst biological (agent and host(s)), environmental, economic and social factors which can affect the emergence and spread of an infectious disease is required. This extension of the epidemiological triad, which incorporates an ecological approach, has been termed the "episystem of a disease" (Tabachnick, 2003, 2010) and is an example of a contemporary whole systems approach to biological investigations (Matthews and Haydon, 2007) which is applied to such diverse fields as obesity management in humans (Egger and Swinburn, 1997) and the prevention and control of emerging infectious disease in both human and animal populations (Wilcox and Gubler, 2005).

The premise behind infectious disease control programmes at the population level is to reduce the maximum reproductive potential of the infectious agent (summarised in the basic reproductive number or R_0, the expected number of secondary cases produced by a single infected individual in a completely susceptible population (Anderson and May, 1991)) so that onward transmission of infection is prevented. In order to reduce R_0 to a value below which the infectious agent will not spread in a population ($R_0 < 1$), it is important to consider the episystem of a disease. While certain diseases may be controlled by a singular modification to their episystem (e.g. enhanced host immunity to control poliomyelitis), others will require a more concerted effort, taking into account all components of the episystem that affect the behaviour, contact patterns and susceptibility of the hosts and the infectivity of the agent.

In this review we discuss, from an episystem perspective, how bovine tuberculosis (bTB) has evaded reductionist methods of eradication in Great Britain (GB) and examine the effect of the episystem of this disease on preceding and imminent control measures. We also examine from an ecological perspective the contentious issue of badger culling and endeavour to reconcile the disparity in results from two large scale badger culling trials in GB and the Republic of Ireland (ROI), whose conflicting outcomes have had far reaching implications for bTB control in GB.

2. The relevance of an episystem approach to bTB control in GB

In GB today, the economic burden associated with the management of bTB in British cattle is one of the greatest challenges facing the animal agriculture industry. This disease has eluded eradication despite more than seventy-five years of concerted effort and is becoming increasingly expensive to manage; in 2008/2009 it is estimated to have cost £108.4 million (Defra, 2010c). While Scotland is now Officially (bovine) Tuberculosis Free (Hall, 2010), bTB remains a serious concern in England and Wales, where since the 1990s, new herd breakdowns have increased at an average rate of 18% per annum (Defra, 2005). bTB has been successfully eradicated from cattle in many developed countries but the existence of wildlife reservoirs has complicated eradication in others (Tweddle and Livingstone, 1994; Schmitt et al., 2002). In GB, as in the ROI, it is the Eurasian badger (*Meles meles*) that has been implicated in bTB persistence (Gallagher and Clifton-Hadley, 2000; Phillips et al., 2003; Corner, 2006; Hone and Donnelly, 2008; Vial and Donnelly, 2011), despite *Mycobacterium bovis*, the causative agent of bTB, being isolated from a wide range of other mammalian species (Delahay et al., 2002; de la Rua-Domenech, 2006; Defra, 2010d). Disease control in GB is further compromised by the badgers' status as a protected species, which includes an explicit prohibition of the culling of badgers for disease control, without a specific licence.

While hypotheses for the continued epidemic of bTB in the face of controls have ranged from environmental contamination (Courtenay et al., 2006) to possible changes in the efficacy of the standard tuberculin test (Smith et al., 2006), the debate in GB has chiefly centred on the role of the badger. In recent years, controversy over bTB in GB has extended to doubts over the cost effectiveness of current control efforts (Torgerson and Torgerson, 2010) and the possibility of a reintroduction of badger culling to supplement cattle control strategies and vaccination (Defra, 2010b). The mounting costs, increasing incidence and geographical spread of infection in cattle and the conflict surrounding former, current and potential control programmes demands that bTB be examined in a new light, in order to advance our knowledge of the intricate nature of this disease and specifically examine how this approach can assist in the development of new control programmes for bTB in GB.

3. The effect of the episystem of bTB on reductionist methods of disease control

An episystem approach to disease control involves developing an understanding of not just the individual attributes that lead to persistence of infection, but how these factors are inter-related, how perturbing any one element influences others, and how these inter-relationships can be exploited to control a disease where a more naïve approach may fail. To begin our examination of the episystem of bTB we consider how the inherent complexities of the entire episystem (Fig. 1) have led to the failure of conventional control measures to suppress the spread of the disease in GB and hindered the development of new management programmes.

3.1. Selective culling of cattle

Selective culling of cattle has been at the forefront of many of the bTB eradication campaigns in GB since they began in the 1930s (Krebs et al., 1997). Cattle test and slaughter programmes have been effectively applied to the eradication of bTB in certain countries (Tweddle and Livingstone, 1994) and such a programme was responsible for the near eradication of bTB in GB in the 1960s but