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Deer and pigs as hosts of bovine tuberculosis, and their potential use as sentinels of disease presence

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ABSTRACT

Feral pigs and wild deer often have the highest local prevalences of bovine tuberculosis (Tb) of any of the wild animal species present in infected areas. Despite this, pigs have long been regarded as 'spillover' hosts that become infected mainly by scavenging infected carrion, rather than by transmission from other pigs. Deer, in contrast, appear capable of independently sustaining the disease when their densities are high, but not when they are low. Most infection in wild deer in New Zealand also appears to be spillover infection. As spillover hosts, both pigs and deer have the potential to be used as sentinels for identifying when and where Tb occurs in local possum populations. Within the constraints of local availability, pigs appear to be potentially more valuable as sentinels than deer.

Keywords: bovine tuberculosis; brushtail possums; deer; detection of disease; host status; pigs; sentinel; *Cervus elaphus*; *Mycobacterium bovis*; *Sus scrofa*; *Trichosurus vulpecula*

INTRODUCTION

Eradication of bovine tuberculosis (Tb) has been successfully achieved in many countries, including Australia (Cousins & Roberts, *in press*), but in New Zealand the involvement of brushtail possums (*Trichosurus vulpecula*) as a true maintenance host (one capable of independently sustaining the disease) has so far prevented Tb eradication (Coleman & Caley, 2000). Infection has also been found in a wide range of other introduced mammals but most have an inconsequential role in sustaining the disease (Cooke *et al.*, 1999). However, high prevalences of Tb have sometimes been recorded in feral pigs (*Sus scrofa*) and wild red deer (*Cervus elaphus*) (Lugton, 1997), so a key question during the 1990s has been to resolve what role wild deer, in particular, play in maintaining Tb in wildlife. I briefly review the evidence on host status for these two species, and then explore their potential use as "sentinels" for detecting the presence of Tb in possums.

HOST STATUS

Deer

Tuberculosis in wild deer in New Zealand was first recorded in 1956 on the West Coast of the South Island (Livingstone, 1994, cited in Coleman & Caley, 2000). Subsequently, Tb was isolated from low numbers of wild deer during the early 1970s, increasing to > 60 by 1980 (de Lisle and Havill, 1985). The first recorded infection in farmed deer was in 1978 (de Lisle and Havill, 1985). By the late 1980s over 300 herds were infected, but intensified Tb management reduced that to 98 infected deer herds in 1999/00, when 777 tuberculous farmed deer were identified (AHB, 2000a) from a population of about 2 million.

The prevalence of Tb in wild red deer populations in New Zealand (Nugent & Lugton, 1995; Lugton *et al.*, 1998) has sometimes been much higher (>30%) than ever reported in wild and park deer overseas (seldom >5%; Clifton-Hadley & Wilesmith, 1991). Occasional "explosive" outbreaks of Tb on farms (e.g., Griffin *et al.*, 1998) show unequivocally that deer can maintain the disease if deer-to-deer contact rates are sufficiently high. Those outbreaks, and the high prevalences observed in the wild, combined with evidence that Tb could pass from deer to other wildlife

(Mackereth, 1993), led Morris & Pfeiffer (1995) to suggest that deer also fulfilled the requirements for being a true maintenance host. As a consequence, deer were targeted for control by the mid-1990s (AHB, 1996). However, very low infection rates in fawns, even when a high proportion (up to 50%) of their mothers are infected, indicate that deer-to-deer transmission rates in the wild must be very low (Nugent & Lugton, 1995; Lugton *et al.*, 1998). That suggests that most infection in wild deer in New Zealand results from "spillover" infection from another host (presumably possums) rather than from transmission between deer. This spillover hypothesis has since been confirmed experimentally by the large reductions in infection rate in wild deer that have been observed when sympatric possum populations were reduced (Nugent & Whitford, *in press*). That experiment also showed little change in prevalence in older deer born before possum control, indicating that Tb had only a small effect on deer survival. However, some deer are genetically more susceptible to Tb than others (Mackintosh *et al.*, 1998), and terminally ill wild deer have occasionally been observed (Lugton *et al.*, 1998), so the disease does have an effect on deer survival.

The most commonly observed signs of Tb in deer are abscesses (lesions) in lymph nodes, which can be up to 20 cm in diameter, but most infected deer have single small lesions that contain few bacilli (Lugton, 1997). The oropharyngeal tonsils appear to be the most commonly infected site in wild deer, but often do not have gross lesions typical of Tb (Lugton *et al.*, 1998). The medial retropharyngeal lymph nodes are the most common site for gross lesions (Hathaway *et al.*, 1994). Experimental infection via the tonsils closely mimics the normal progression of Tb in deer (Mackintosh *et al.*, 1993). This supports Lugton *et al.*'s (1998) contention that oral ingestion via the tonsils is the main route of infection in deer. They suggest that deer-to-deer transmission on farms results mostly from direct contact with bacilli-laden discharges from lesions that drain to the outside of a small number of infected deer. For wild deer, infection may most commonly result from investigation of sick tuberculous possums (Sauter & Morris, 1995). Transmission from possums to deer has been demonstrated under natural conditions (Lugton *et al.*, 1997).

Pigs

Tuberculosis has long been identified in domestic pigs associated with infected cattle. For feral pigs in New Zealand, the earliest reports date back to 1964 (Ekdahl *et al.*, 1970). de Lisle (1994) isolated *M. bovis* from 105 feral pigs between 1987 and 1993. Up to 33% of pigs in Central Otago have been found to be infected (Wakelin & Churchman, 1991; Knowles, 1994), while Lugton (1997) reports a 96% prevalence in feral pigs from two areas in the North Island. Despite these high prevalences, pigs are regarded as spillover rather than maintenance hosts. Nowhere in the world has Tb persisted in pigs in the absence of infection in other species. In the Northern Territory in Australia, for example, pigs once shared their range with infected cattle (*Bos taurus*) and water buffalo (*Bubalus bubalis*), and many (48-85%) of the pigs surveyed between 1958 and 1976 had lesions resembling Tb (McInerney *et al.*, 1995). After 1985, the bovids (but not the pigs) were controlled to low density and the Tb prevalence in pigs fell dramatically (McInerney *et al.*, 1995).

Of all the domestic species, the pig is the most susceptible to Tb, particularly when young (see review by Lugton, 1997). Older pigs are much more resistant, with the disease typified by fibrosis and calcification, and with lesions tending to regress as the pig ages. Lesions are most common in the head and mesenteric lymph nodes, and although lesions are seldom present in the tonsils, Lugton (1997) argues that oral ingestion via the tonsils is the main route of infection. Most authors agree that wild pigs in New Zealand typically become infected through scavenging infected possum carcasses and other carrion.

POTENTIAL USE AS SENTINELS

At present there is no easy way of assessing whether Tb is still present at low levels in particular populations of possums, the main maintenance wildlife host in New Zealand. However, as spillover hosts do not by themselves independently sustain Tb long-term, they can potentially be used as "sentinels", to help identify where and when Tb is likely to be, or have been, present in local possum populations. That concept has recently gained more attention in New Zealand because many areas now have too few possums and/or too few farmed cattle and deer to provide adequate surveillance (AHB, 2000b).

When pigs and deer are used as sentinels, the probability of detecting Tb in an area will depend on how many are sampled, the proportion of the area covered by each animal (coverage), and their sensitivity as a "sensor" (susceptibility to, and detectability of Tb). For each individual, coverage will reflect life span and home range size - all else being equal, animals with the largest range sizes and the longest life spans will have had the greatest exposure to potential infection. Susceptibility and detectability will depend on the frequency of potentially infectious encounters with Tb sources, the proportion of those encounters that result in actual infection, and the duration of detectable infection.

Possums make poor sentinels. They have small lifetime home ranges (typically averaging <1-5 ha, but occasionally up to c. 30 ha; Cowan & Clout, 2000), and a short survival period (2-6 months) for animals with clinical infection (Morris & Pfeiffer, 1995; Coleman & Caley 2000). Their small home range size, in particular, means almost all of

the possums in an area would have to be surveyed to be confident that Tb is not present.

Home range sizes for pigs and deer are much larger. For red deer in continuous forest annual range sizes are likely to be 1-5 km² for females, and double that for males (Nugent, 1993). Where cover is sparse, range size can be up to 110 km² (Knowles, 1997). Pig range sizes are similar, with similar variability between habitat types, ranging from about 1 km² in good habitat (McIlroy, 1990) to over 150 km² in the Pisa Range, Otago (Knowles, 1994).

Pig and deer populations in New Zealand are almost all heavily harvested, so survival rates are likely to be shorter than for possums in uncontrolled populations, but perhaps broadly similar to those for controlled possum populations. In the northern South Island, 70% of a hunter-killed sample of pigs were <1 year old, with a mean age of 11 months (Dzieciolowski & Clarke, 1989). In contrast, the youngest age structure known for deer is for a hunter-killed sample of fallow deer (*Dama dama*) in the Blue Mountains, Otago, which had a mean age of 2.4 years (Nugent *et al.*, 2001). A typical hunter-killed sample of deer therefore represents a greater exposure time than a similar number of pigs.

Pigs appear to contract Tb from possums more readily than do deer, resulting in higher prevalences in pigs than in deer from the same area. In the central Hauhungaroa Range, where infected possums are common, all of the five adult pigs inspected have been infected (G. Nugent, unpubl. data) compared with only 37% of 30 adult deer (Coleman *et al.*, 2000). Likewise, 96% of 33 pigs (all ages) in the Castlepoint area, Wairarapa, were infected, compared with about 30% of 30 deer (all ages) (Lugton, 1997). In Hochstetter Forest, Westland, only 11% of 115 deer killed in 1997-99 were found to be infected (Ramsey *et al.* 2001 unpublished report), whereas all of 15 pigs released into the area in February 2000 became infected within a few months (G. Nugent, unpubl. data). Few wild deer become infected in their first year, and prevalence increases with age, faster in males (Nugent & Whitford, 2001). In contrast even piglets 1-2 months old have been found infected (e.g., Knowles, 1994).

Lugton *et al.* (1998) found that three quarters of infected deer had no visible lesions, and in an ongoing study, gross lesions were seen in only about 20% of infected wild deer in Westland (G. Nugent, unpubl. data). Mycobacteriological culture of key tissues (pooled tonsils and retropharyngeal lymph nodes) would therefore improve detectability in deer. In pigs, gross lesions are detectable in most infected animals when overall prevalence is high, and the head lymph nodes appear to be far more consistently involved than for deer from the same area (Lugton, 1997). This makes Tb infection more readily detectable in pigs, especially when only the head is available for inspection and when detection is based solely on the presence of visible lesions.

Other key factors affecting the utility of pigs and deer as sentinels are the distribution and density of each species. These factors determine availability and the cost of obtaining a sample. Pigs tend to be most common in marginal scrubland and pine forest areas, while deer are now confined mainly to tall native forest. The main areas in which wild deer, but not pigs, are common are the lower central North Island (mainly the Ruahine Range), most of the West Coast, western Canterbury, and Fiordland (Fraser

et al., 2000). The total population of wild deer is thought to be about 250,000, with an annual harvest of about 75,000 and an average density in forests of 3-4/km² (Nugent *et al.*, 2001). Feral pigs occupy, in total, about 93,000 km² (Fraser *et al.*, 2000). Key areas not well covered by deer, but where pigs are found, include northern Northland, Coromandel Peninsula, Taranaki and parts of northern Canterbury, eastern Otago, and central Southland. The national feral pig harvest in 1988 was estimated to be 99,000 (Nugent, 1992), and the breeding population is likely to be similar. The average density of pigs is therefore likely to be 1/km². The costs per kill for pigs are, on average, substantially lower than for deer (Nugent, 1992).

DISCUSSION

It is increasingly clear that, at the densities at which they occur in the wild in New Zealand, red deer are primarily “spillover” hosts that become infected mainly through some interaction with Tb-infected possums. The threshold deer density at which deer-to-deer transmission rates reach maintenance host levels is not known. However, it appears to lie between the densities for red deer in New Zealand (almost always < 10/km²; Nugent *et al.*, 2001) and those for wild white-tailed deer (*Odocoileus virginianus*) in Michigan where Tb has recently spread independently of other hosts (19-23/km²; Schmitt *et al.*, 1997), assuming that the two species are equivalent hosts.

As spillover hosts, the occurrence of infection in both pigs and deer identifies the presence (or former presence) of an infection source somewhere within their lifetime range. In terms of relative susceptibility to, and detectability of, Tb infection, older pigs and deer tend to make better sentinels than younger animals, because of their longer exposure time (and low losses due to Tb-induced mortality); conversely fawns (deer < 12 months old) make poor sentinels. Male deer may be better sentinels than females, presumably partly as a consequence of their greater home range size. However, because of their smaller home ranges, the discovery of infection in a female provides a more precise spatial indicator of an infection source.

All else being equal, pigs are likely to be much better sentinels than deer. They have higher infection prevalences than deer from the same area, equally large home ranges, and, once infected, appear able to carry and show detectable signs of disease for much of their lives. They are also more commonly killed in or near farmland than deer, and nationally more pigs are killed than deer. However, differences in habitat use and local abundance mean availability (and therefore the cost of sampling) will often override these epidemiological characteristics. Deer, for example, are usually more abundant in remote native forest areas so will be most useful there. As an example of their value as sentinels, infected deer pinpointed two areas in the eastern Hauhungaroa Ranges that had not been treated in a 1994 possum poisoning operation (Coleman *et al.*, 2000).

The eradication of Tb from New Zealand will require increased surveillance of Tb in wildlife (AHB, 2000b). Monitoring of disease presence in pigs and deer will undoubtedly contribute to that. Already, many of the deer shot each year are sold to game packing houses where they are inspected. The merit of a proposal to expand that

surveillance to include pigs and deer shot by recreational hunters (Ramsey *et al.*, 2001 unpublished report) hinges on the cost of that relative to the cost of directly surveying possums.

The extreme test of any surveillance programme will inevitably be when Tb persists in possums at a single focus in an area. Assuming that the point of infection is within the home range of a group of pigs, the probability of detectable infection in each pig depends on the number and distribution of possum carcasses, the ease with which pigs find them, and the density of pigs. Because the survival times of infected possums are substantially less than one year, there will be more infected possum carcasses available over the course of a year than infected possums alive at any one time. One intriguing possibility is that the number of infected pigs in an area could sometimes substantially exceed the number of infected possums. This could occur if each encounter by a group of pigs with an infected possum carcass resulted in the simultaneous establishment of infection in a large number of pigs. Even if there are fewer infected pigs than infected possums, however, surveying pigs could still often be more cost-effective than surveying possums. The cost advantage will depend on the cost of obtaining pigs relative to the cost of surveying the equivalent proportion of the possum population, and, inversely, on the ratio of infected pigs to infected possums (with the important caveat that the pig population range includes all of the possum range).

In summary, pigs, in particular, appear to have substantial potential for use in detecting Tb presence in wildlife, as there are both practical and theoretical grounds for believing that pigs could provide a more cost-effective “sensor” of Tb presence in possum populations than the possums themselves. Deer may often also be valuable sentinels, but are likely to be less cost-effective in this role than pigs.

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